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CLASSES AND TYPES OF INTRASPECIFIC INCOMPATIBILITIES[1]

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In respect to the locus of sexual reproduction in the life cycle and to the scope, action and genetics of the modifying factors of incompatibilities, there are three main classes of incompatibilities which may be designated as follows:—

I. *The diplont-haplont class.* In the flowering plants the inhibiting effects of self- and cross-incompatibilities occur chiefly during reactions between the diploid tissues of the pistils of flowers of the sporophytic generation and the haploid pollen tubes of the alternating gametophytic generation.

II. *The haplont-haplont class.* In the fungi the reactions of incompatibilities occur in the interrelations between individuals that are haploid, bisexual and gametophytic.

III. *The diplont-diplont class.* In the ciliates among animals the reactions of incompatibilities operate chiefly in the relations of selective conjugation between individuals that are bisexual and diploid and hence comparable to the sporophytic generation in plants.

I. The Diplont-Haplont Incompatibilities in Flowering Plants

Self-incompatibility. A self-incompatible individual must of necessity be bisexual (hermaphroditic). The identification and study of incompatibilities is most defi-

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nite when there are no conditions, such as herkogamy and dichogamy, which limit or prevent the necessary association of elements of sexual reproduction. The flowering plants included in this discussion, unless otherwise stated, have perfect homomorphic flowers without any conditions or developments which limit or prevent self-, close- and cross-pollination.

Self-incompatibilities ("self-sterility") were recognized some 150 years ago in the early studies of "flower pollination" and hybridization. Darwin and his contemporaries observed in a number of species that the pollen of stamens may be inactive on the stigma of the same flower. But Darwin (1876) did not recognize that there is also cross-incompatibility among plants that have homomorphic flowers. He stated in 1876 that "We may confidently assert that a self-sterile plant can be fertilized by the pollen of any one of a thousand or ten thousand individuals of the same species." The authority of this statement no doubt greatly delayed recognition of cross-incompatibilities.

Intraspecific cross-incompatibilities were first definitely recognized and related genetically to self-incompatibilities by Correns (1912). But his interpretation considered that the reactions are determined by diploid genetic constitutions.

The first satisfactory evaluation of both the reactions and the genetic determination of self- and cross-incompatibilities in homomorphic flowering plants was by Prell (1921). He recognized that the incompatibility reactions are between *diploid* tissues of the pistils and *haploid* pollen tubes. He postulated a single allelic series of multiple, *oppositional* genetic factors (O_1O_2; O_1O_3; O_1O_4; O_2O_3; &c.). The primary reaction was considered to be the independent self-antagonism of one factor (O_a or O_b) in a haploid pollen tube with the same factor in the diploid (O_aO_b) tissues of the pistil either in selfing or in crossing. In self-incompatibility and in complete cross-incompatibility the two haploid classes of pollen together

possess both of the incompatibility factors present in the pistils. Thus the two factors in the diploid plant are allelic but merely oppositional in position. Prell considered (1) that the self-incompatible plants are normally heterozygous for the special factors; (2) that there is what may be called hidden incompatibility and elimination of the genotype of the seed parent in the progeny when two parents possess one factor in common; (3) that there is elimination of the genotypes of both parents in a progeny when there is no common factor; and (4) that there may be induced or anaphylactic reactions due to cytoplasmic influence.

Applications of Prell's hypotheses were first made in experimental studies of incompatibilities in flowering plants of which reports by several persons were published in 1925, 1926 and 1927. The data demonstrated various critical features of behavior postulated by him.

1. THE PERSONATE MODE OF INCOMPATIBILITIES

The term "personate" was applied by Correns (1928) to what is the simplest mode of diplont-haplont intraspecific incompatibilities in homomorphic bisexual flowering plants. All the important and critical features of this mode have now been demonstrated and may briefly be summarized as follows:—

A. *In regard to mating reactions:*—1. The individuals are self-incompatible (S). 2. There are at least *three*, and often more, mating groups in the population of a species. 3. The members of each group are cross-incompatible. 4. As a rule the members of any two of the mating groups are cross-fertile.

B. *In regard to genetic relations and reproduction:*—1. Both self- and cross-incompatibilities are determined by the same genetic mechanism. The simplest personate mode in flowering plants involves at least three factors (usually designated S_1, S_2 and S_3). 2. The progeny of two plants comprise either two or four mating groups. 3. When there are two groups in a progeny there is hid-

den incompatibility which gives the elimination of the genotype of the seed parent and the appearances of a third genotype, as I (S_1S_2) $\times$ II (S_1S_3) = II (S_1S_3) and III (S_2S_3). This is due to the self-incompatibility reaction of the common factor (S_1). 4. When there are four mating groups in a progeny there is elimination of both parent genotypes:—I (S_1S_2) $\times$ IV (S_3S_4) = II (S_1S_3); III (S_2S_3); V (S_1S_4); and VI (S_2S_4). 5. The simplest or minimum sustaining population is one with three S factors and three mating types (S_1S_2, S_1S_3, S_2S_3). The progenies of the six reciprocal matings will, under natural free cross-pollination, provide interpolations that result in a balance of genotypes. 6. A population in which there are four S factors will consist of six mating groups, there will be thirty reciprocal cross-matings, and the reciprocations will tend to balance the different mating genotypes. 7. The incompatibilities effect selective reproduction *within* the populations of a single species. They are entirely distinct from interspecific hybridizations. They are intraspecific. 8. The mating is *bi-genotypic.* Self- and intra-genotypic reproductions are eliminated, and homozygotes for S factors do not appear normally.

Adequacy of the genetical analyses. In various species, or in such segments of them as have been studied, there are definite and effective expressions of the incompatibilities by a single allelic series of S factors. It is, however, to be recognized that the quality and strength of the various S factors differ not only among different species but in a single species. Such differences in expression as (a) end-season fertility, (b) cyclic incompatibility, (c) differences in the observed behavior of pollen tubes, (d) partial or feeble fertility, and (e) border-line action of certain factors have been recognized.

The fundamental nature of incompatibilities in relation to the fertility of sexual reproduction. It is recognized that in the personate mode the S factors comprise an allelic pair in each of the diploid individuals that mate.

Since plants which mate are different in one or in both *S* factors it is often considered that these factors effect fertility when in this condition. Also in various hybridizing relations between species, an *S* factor of the one is often represented as allelic to a fertility factor of the other. I am convinced that this is not an adequate and correct evaluation. As early as 1931 it was suggested (Stout, 1931) that the special factors of incompatibilities are superimposed on the fundamental mechanism of intraspecific fertility in a species. This view has again been stated in connection with a report that incompatibility factors may be inactivated when there is a change to tetraploidy (Stout, 1945).

A further consideration of this matter may now be made as follows:—1. There are no special sexual organs or elements exclusively involved in the reactions of incompatibilities. They operate by inhibiting an action that is already established as a necessary step in sexual reproduction. 2. Incompatibilities exist in certain species of various families of flowering plants; but, of several closely related species that readily hybridize and are very similar, some may have incompatibilities and others may have none. This emphasizes the fact that no aspect of these incompatibilities is an obligate concomitant of sexual reproduction. 3. There is general agreement that *S* factors are *inactive* in effecting incompatibility unless there is self-interaction. 4. There is evidence that inactivations of *S* factors are increased in polyploid flowering plants; and that there may be complete inactivation which is transmitted to seed progenies. 5. Incompatibility reactions may be reduced or avoided by special means such as removing secretion from stigmas or by premature pollination. In cyclic incompatibility there is fertility in the mid-season of flowering. When incompatibility factors do not operate effectively there is fertility of interspecific sexual reproduction.

It is concluded that incompatibilities are physiological and inhibiting reactions that are superimposed on, and secondary to, the more fundamental mechanisms and fea-

tures of sexual reproduction which will be referred to as *residual fertility*. We may consider that special genetic factors effect epistatic incompatibility reactions and that when these are inactive there is the action of intraspecific fertility for which every homomorphic bisexual individual is fully equipped.

2. THE ASSOCIATE MODE OF INTRASPECIFIC INCOMPATIBILITIES

The interpretation of what is called the associate mode of incompatibilities was postulated by Kakazaki in 1930 to explain the complicated reactions which he observed in cabbage (*Brassica oleracea*). His conceptions have been rather fully evaluated, tested, and applied in connection with the behavior of incompatibilities in a diploid variety of garden petunias known as Rosy Morn (Stout, 1938). The recognition of the features and genetics of this mode aids greatly in the evaluation of incompatibilities that do not conform fully to the personate mode.

The features which characterize this mode of incompatibilities, in comparison with those of the personate type, may be summarized as follows:—

(A) *In respect to reactions of mating types:*—1. The population consists of self-incompatible (*S*) and self-fertile (*F*) individuals and mating groups. 2. There are numerous *S* and *F* genotypes in the entire population. 3. There are both cross-fertility and cross-incompatibility between *F* genotypes. 4. There are reciprocal differences in reactions. 5. The members of a group which react uniformly with various others may, when more widely tested, prove to be composed of two or more minor groups. Thus a mating group may be polygenotypic. 6. The determination of the ultimate mating groups often requires numerous collateral and reciprocal testings.

(B) *In respect to progenies of the various matings and their reaction groups:*—1. The number of mating types in different mating progenies range from one to as many as 12. 2. The selfed progenies of *F* plants segregate into both *F* and *S* genotypes. *F* plants do not breed true. They carry factors that are inactive or that exhibit

hidden incompatibility in both selfing and in cross-fertility. 3. The progenies of reciprocal crosses differ in the number and the character of the mating groups. 4. The eliminations in a progeny effected by hidden incompatibility may be as many as six genotypes. 5. The eliminations complicate genetical analysis and effect complicated alternation of parent genotypes in a succession of line progenies. 6. The interpolations of genotypes of the various progenies are complex in respect to balance in populations.

(C) *Evaluations of reactions and genetic determinations:*—1. The evaluation that best accounts for all the reactions and progenies considers that there is one allelic series of three S factors (S_1, S_2, and S_3) and one allelic series of two special oppositional factors called T_1 and T_2, which favor fertility. 2. The reactions in haploid-diploid relations are $SSTT \times ST$. There is independent self-interaction for each factor. T factors interact to favor pollen-tube growth when they are alike in both pistil and pollen; S factors are inhibiting when alike; otherwise there is inactivation. But there are one S and one F factor in each pollen grain and their reactions are often in conflict; and there are neutral and epistatic relations in regard to the growth of the pollen tube. 3. This interpretation recognizes that not only incompatibility factors but also special factors which favor fertility may be superimposed on fundamental intraspecific fertility. 4. Except for the selfing and intra-crossing among each of the F genotypes, which do not breed true, all reproduction is bi-genotypic. For further discussion and experimental data and for charts showing patterns of population matings, hidden incompatibility and numerous patterns for progenies, reference may be made to a previous publication (Stout, 1938).

3. MORE COMPLEX MODES OF INCOMPATIBILITIES IN TETRAPLOIDS

A brief mention may be made of the more complex modes of incompatibilities that have been recognized. It

is significant that these have been found especially, if not chiefly, in natural species and cultivated plants that are considered to be polyploid. In some cases at least these are of such long existence that the processes of meiosis have become standardized on a bivalent basis. Some of these amphidiploid species have evidently arisen from diploids that had personate incompatibility while others arose from diploids which had an associate mode.

The pollen of such tetraploids contains at least two *S* factors instead of one, and in many cases these are different. But a pollen tube is a single unit of growth and reaction and it is not able to exhibit two different reactions at the same time. Its two or more *S* factors, and also any special fertility factors that are present, may supplement each other in the same effect, compete in different reactions, exhibit a complementary effect, and produce new inhibitions or inactivations. There are the combined reactions in pollen grains, in tissues of pistils, and in the relations between the two. Reactions between 4n pistils and 2n pollen tubes provide opportunities for complex qualitative and quantitative interrelations. Every aspect of incompatibilities and fertilities seen in the diploids are present in tetraploids in various degrees of increased complexity.

Amphipersonate incompatibilities. Several earlier studies of *Verbascum phoenecium* indicate that the pattern reactions of progenies are not characteristic of the personate mode. More recently it has been considered that the members of this species are allotetraploid, that they possess two different allelic series of *S* factors (S_aS_b Z_aZ_b, &c.) and that there are multiple factors in each series in all possible homozygous and heterozygous combinations. When two *S* plants, that are heterozygous for both pairs of *S* factors and have no *S* factor in common, are cross-bred the progeny can comprise as many as 16 genotypes. When a progeny of no more than 20 plants are obtained and tested certain mating groups in their pattern may be polygenotypic. It appears that

Verbascum phoenecium may be called amphipersonate in its incompatibilities.

Amphiassociate incompatibilities. Cardemine pratensis may be considered as a species which has amphidiploid associate incompatibilities. From the results of studies with this species, Correns in 1912 first definitely recognized intraspecific cross-incompatibilities in homomorphic flowering plants and suggested a genetic status. But this was based on conceptions of dominance and recessiveness of Mendelian factors and the "sterility" was considered to be a diploid character. The diplont-haplont relation was not then conceived and Correns considered that the plants which he studied could be placed in only four mating groups.

Beatus (1934) has more recently studied this species and his reports indicate a tetraploid associate mode of incompatibilities which involves multiple factors in each of two allelic series of S factors and also in each of two allelic series of F factors. He postulates all combinations of heterozygocity and homozygocity in the various individuals for each factor of the four series. On this basis as many as 16 genotypic classes of pollen may segregate in the pollen of a plant or in the egg cells in ovules and as many as 256 genotypes are possible in the offspring of two parents.

Evaluations. You may feel that such complexities tax one's imagination and prohibit complete experimental demonstration. They do, but various of the most essential features of such complexity can be and have been determined. In comparison with the more simple personate and associate modes these polyploid cases exhibit greater complexity in all the features of incompatibilities and fertility such as:—the number of mating groups; border line and indefinite reactions; hidden incompatibilities; indirect heredity; elimination and rotation of genotypes in line bred progenies; increase in inter-genotypic incompatibility; and increase in polygenotypic major mating groups.

It is obvious that polyploidy increases the number of allelic series and multiplies the number of factors in tissues of pistils and in pollen grains. This compels multiple complementary reactions instead of the single-factor reaction in a pollen tube of a personate diploid.

Increased fertility. One feature of behavior in the incompatibilities of polyploids merits special mention. Repeatedly the amount of cross-fertility exceeds expectations that are based on the effective independent self-interaction of each of the various S factors that are present. Various investigators have considered that a polyallelic relation may be fertile if there is a *difference in only one* of the incompatibility factors. For example an amphipersonate relation of $S_1S_2Z_1Z_2 \times S_1S_2Z_1Z_3$ may be fertile on account of the functioning of S_1Z_3 and S_2Z_3 pollen. Thus it may be considered that the inaction of one factor (S_3) in the pollen may be accompanied by the inactivation of another S factor which is common in both pistil and pollen (S_1 or S_2). Such inactivations automatically give residual fertility the opportunity to function.

4. INACTIVATION OF INCOMPATIBILITY FACTORS IN POLYPLOIDS

The complete inactivation of all incompatibility factors has recently been demonstrated in autotetraploids of *Petunia axillaris* that were obtained experimentally from known personate diploids (Stout and Chandler, 1941; *idem,* 1942; Stout, 1945). Tetraploid branches were obtained on each of 15 different diploid plants by treatment with colchicine. The self-pollinated flowers of all these branches produced fine capsules well filled with viable seeds, while the flowers of the diploid branches on the same plants remained self-incompatible. This inactivation of incompatibility factors was inherited in all seedlings grown from the selfed seed of tetraploid branches, and also in all of over 300 seedlings of two later generations. Also several thousand of the cross-relations between tetraploid plants (intra-series, inter-series, 4n parents and 4n progeny, etc.) were tested by con-

trolled pollinations. In every one of these intra-tetraploid cross-relations as well as in the selfed-relations many viable seeds were produced. The change from incompatibility to complete residual fertility occurred in the somatic tetraploidy of known personate diploids in which the two S factors were doubled ($S_aS_aS_bS_b$) and it continued in the *selfed* progeny.

In Trifolium repens. In similar studies with *Trifolium repens* recently reported by Atwood (1944) self-fertility first appeared in the seedling progenies derived by crossing two tetraploids which possessed no common S factor (the diploids from which they were obtained were (S_1S_2 and S_3S_4). Of the 29 seedlings of the first 4n progeny ($S_1S_1S_2S_2 \times S_3S_3S_4S_4$) three were self-incompatible and 26 were self-fertile and also cross-fertile. These results indicate that some of the recombinations (assumed to comprise either three or four S factors; as $S_1S_1S_3S_4$ or $S_1S_2S_3S_4$) effected self-fertility while others (assumed to involve two S factors as $S_1S_1S_2S_2$) continued with self-incompatibility.

Retention of self-incompatibility in tetraploids. But there are other reports which indicate that self-incompatibilities and also cross-incompatibilities may continue in tetraploids experimentally derived from self-incompatible diploids. Howard in 1942 reported that all tetraploid branches derived from *Brassica Rapa, B. campestris* and *Raphanus sativus* which he studied were self-incompatible. Hecht (1943) reports that tetraploids of *Oenothera rhombipetala* grown from colchicine treated seeds obtained from S plants were all self-incompatible, that the seedlings obtained from crosses of two such plants were self-incompatible, and that cross-incompatibilities and cross-fertilities continued in the seed-grown progenies.

Thus the tetraploids of some species exhibit complete inactivation of S factors while others do not. The basis for this is, no doubt, that there are differences in the quality and strength of the heredity factors themselves. Experimental studies of known tetraploids in comparison

with their known parents will no doubt provide data for more adequate evaluations of the principles involved in the fundamental properties of *S* factors, especially in regard to inactivations.

5. Cytoplasmic Determination of Pollen-Tube Reactions in Capsella Grandiflora

The early studies of incompatibilities in this species indicate that there are few mating groups but a rather complex genetic behavior in the segregations in progenies. In 1936 Riley (1936) reported that there are three intra-incompatible but cross-fertile groups, which agrees with a minimum sustaining population of the personate mode. But the patterns of mating groups in the progenies were quite different. The results indicated that one group ("A") is poly-genotypic and composed of three genotypes (*Tt*ss; *Tt*ss; and *Tts*s); that group "C" is bi-genotypic (*tt*ss; *tt*ss); and that group "B" is monogenotypic (*ttss*). This evaluation considers that there are two allelic series each having two incompatibility factors, that the four factors have successive relative epistatic powers both within a series and in complementary reactions, and that all the pollen of any individual plant has the same reaction due to cytoplasmic transmission of the diploid character of that individual. This effects a diploid-diploid relation.

The recombinations in the progenies of all fertile matings give a population of six genotypes which however exhibit only three mating groups.

The features of epistatic relations in complementary reactions may prove to be rather frequent not only in diplont-diplont relations but also in haplont-haplont relations. The feature of cytoplasmic determination of pollen-tube reactions may be frequent in the incompatibilities of flowering plants.

II. Haplont-Haplont Intraspecific Incompatibilities in Fungi

In the fungi the locus of both vegetative activity and sexual reproduction is in the haplophase of the life cycle.

This automatically reduces the genetic determination and expression of incompatibility reactions, as of other segregating characters, in each haplont to only one factor of any allelic series or to complementary reactions between one such factor of each of two or more diploid allelic series.

Mating types which involve incompatibilities and effect selective reproduction in fungi are well exemplified and most extensively known in various species of Hymenomycetes, chiefly through the experimental studies made by Bensaude, Vandendries, Brunswick, Hanna and Kniep. Brunswick in 1924 recognized that the failures in mating reactions involve self-sterilities similar to the oppositional reactions postulated by Prell. But Kniep (1928) and more recently Buller (1941) have applied the doctrine of multiple sexes and unisexual heterothallism.

1. INCOMPATIBILITIES IN HYMENOMYCETES

Bipolar incompatibilities with multiple mating groups. In the simplest mode of haplont-haplont incompatibilities, as in *Coprinus comatus,* a sustaining population comprises two mating groups, but the entire population may comprise several such bipolar groups (S_1 and S_2; S_1 and S_3; S_2 and S_3; S_4 and S_5; &c). These may be isolated as geographical races. The members of each mating group do not copulate, and for them there is cross-incompatibility, as S_1 with S_1. But when members of any two mating groups have the opportunity to copulate there are fusions of mycelia which effect reciprocal cross-fertilization except when two races are alike in one (S_1 and S_2 with S_1 and S_3) or in both of the factors.

When the sustaining population of a species comprises only two mating types the mating appears superficially like unisexual heterothallism that is due to genetic segregation of physiological maleness and femaleness or of realizator factors in meiosis. But when there are multiple mating types one must fully evaluate the condition of bisexual heterothallism that involves the action of multiple factors which effect intraspecific incompatibilities.

When the genetic "sex factors" assumed by Kniep are assigned as incompatibility factors the reactions fall into perfect accord with those of the personate incompatibilities in the diplont-haplont relations with the single difference that the mycelia of the fungi are haplonts.

Tetrapolar incompatibilities. Kniep's data for the fungus *Schizophyllium commune* reveal that a sustaining population may comprise two pairs of cross-fertile mating groups but the members of each pair are cross-incompatible with both of the other pair. Also the genetical analysis revealed that the progeny of any cross-fertility segregates into all four mating groups.

Kniep's evaluation considers that there are two allelic diploid series of sex factors which give haploid segregations of two females (*AB* and *Ab*) and two males (*ab* and *aB*); that *AB* × *ab* and *Ab* × *aB* are inter-sexually fertile; that *AB* × male *aB* is sterile. The diploid of any fertile relation is *AaBb*.

Treated as incompatibilities between bisexual haplonts the genotypic diploid constitution is $S_1S_2Z_1Z_2$ and the haplont genotypes are S_1Z_1; S_1Z_2; S_2Z_1; S_2Z_2. In two combinations ($S_1Z_1 \times S_2Z_2$ and S_1Z_2 and S_2Z_1) there are no self-interactions and residual fertility operates. In the combinations $S_1Z_1 \times S_1Z_2$ and S_2Z_1 and also $S_2Z_2 \times$ S_1Z_2 and S_2Z_1 there is incompatibility effected by one common factor. The incompatibility factors segregate in meiosis to give four kinds of haploid hermaphrodites; there is only *one diploid genotype and it is heterozygous* for both allelic pairs of incompatibility factors.

Multiple races with tetrapolar incompatibilities. These exhibit the extension of incompatibilities in a species by the genetic action of multiple alleles in one or in both of *two allelic series* of *S* factors. In the species *Coprinus lagopus* (= *C. fimetarius*) Brunswick determined 729 genetically different haplonts and soon thereafter 24 different tetrapolar races of this species were recognized by Hanna (1925). Within each race the patterns of the reactions and of the genetic segregations are as in

Schizophyllium commune. But when these different races are interbred all inter-relations are fertile. On Kniep's and Buller's assumptions there are many kinds of males and many kinds of females and in the inter-relations between races any female group is cross-fertile not only with all males but with all other females; and any male group is cross-fertile with the other males of inter-race relations.

Evaluations. Kniep continually interpreted the failures in mating of the mycelia in these fungi as a reaction between two sexes. Species whose monosporous mycelia did not fructify unless mated were classed as dioecious in contrast to those that were self-reproducing and bisexual (homothallic). Multiple mating is, in this view, merely an extension of the mating of unisexual males and females and the non-mating of any two of the same sex. It was assumed that there are numerous quantitatively different males and females which are differentiated by quantitative values of the numerous sex factors that determine both the successes and the failures of copulation.

Brunswick in 1924 rejected this view of Kniep's and considered that the failures in copulation involve *sterility* factors with the action of oppositional factors as postulated by Prell. He noted that the phenomena of mating in these fungi are very similar to the so-called self-sterilities in hermaphrodite flowering plants. It seems rather obvious that this is the correct view.

In evaluating these reactions of mating the first consideration is whether or not a mycelium is functioning as a unisexual or as a bisexual individual. An individual haploid mycelium of the particular species of fungi under consideration must be, it seems to me, recognized as bisexual for the following reasons. The matings are copulations of apparently undifferentiated cells of two mycelia. There are no specialized branches that can be regarded as sex organs. The mycelia intermingle; there are multiple copulations; two cells that copulate come

into close contact and an opening is formed through their walls. The nucleus in each conjugant divides by mitosis and the two sister nuclei become physiologically differentiated in the *first stage of nuclear sexuality.* The one that remains in its cytoplasm may be called female; the other, or male nucleus, migrates into the other conjugant cell. Thus there is an exchange of nuclei. Each conjugant fertilizes or spermatizes the other in the sense that a dikaryotic association of two semi-sexually differentiated nuclei is effected. Such behavior certainly indicates that each haploid mycelium is hermaphroditic at the time of copulation and before there is exchange of nuclei. The reactions of incompatibility are to be regarded as properties of the entire haploid body of each mycelium in their inter-relations. These properties are determined by genetic factors which segregate in meiosis. There may be further fusions of mycelia after dikaryotic association.

Nuclear sexuality, whether of male or female potency or of "realizator" factors, in these particular haploid bisexual and homomorphic fungi is not genetically segregated in meiosis but is a matter of somatic differentiation, as this and many other features of sexuality always are in any hermaphrodite either haploid or diploid.

It seems that many students of the fungi, especially Kniep and Buller, have very generally considered that any species of fungus whose members exhibit mating is haplodioecious and "heterothallic" and that the members are unisexual. This view fails to distinguish between true unisexual heterothallism and bisexual heterothallism which is effected by either dichogamous developments or by incompatibilities.

Further complexities have been noted in the Hymenomycetes, and in other fungi, in both the mating patterns of populations and of progenies; of these mention may be made of the following:—(1) Aversion or barrage reactions (Vandendries and Brodie, 1923; Biggs, 1938) in which one pair of allelic factors in a tetrapolar mating

effect "aversions"; and (2) false clamp connections were also recognized by the authors just noted. But such behavior occurs after fusion. (3) Secondary fusions of mycelia and secondary exchanges of nuclei between dikaryonts and non-dikaryonts which effect the so-called legitimate and illegitimate exchanges of nuclei. (4) Epistatic complementary determination in the completion of factors in haplonts. (5) Presence of groups that are neutral. (6) Presence of apomictic life cycles. (7) Operation of both bipolar and tetrapolar incompatibilities in an inter-breeding population with "Durchbrechungskopulationen."

2. BIPOLAR INCOMPATIBILITIES IN THE RUST FUNGI

Incompatibilities in the rust fungi are well exemplified in the well-known barberry-grain rust, *Puccinia graminis*. Our consideration to-day involves only the evaluation of the barberry phase of the life cycle in which the haploid uninucleated bisexual mycelium accomplishes the fusions which effect the dikaryotic association of male and female nuclei of the dikaryophase of the life cycle.

The individual monosporous mycelium of an infection area in the barberry leaf is haploid and bisexual. The pycnia are somatically differentiated as aggregates of two kinds of branches; (1) those that produce pycnospores which function as male spores and (2) those that function as trichogynes in the process of effecting the dikaryotic association of potential male and female nuclei. There is hence a somatic differentiation of two haploid structures of importance in sexual reproduction and which may be compared, in relative significance at least, to the differentiations of diploid pistils and stamens in a flower or in a composite cluster of flowers.

Cragie (1927; 1931) demonstrated experimentally that in *Puccinia helianthii* and *P. graminis* the pycnospores or spermatia of a mycelium do not function in self-relations and that in respect to the cross-relations there are two intra-cross-incompatible but inter-cross-fertile mating

groups. The mechanism of effecting cross-spermatization is surprisingly like that which effects cross-pollination in flowering plants which have perfect flowers. Secretion forms in droplets on the pycnia; flies feed on this secretion and transport the functionally male pycnospores from one individual haplont to others. The experimental tests revealed that the self-relations and cross-relations between members of a mating group fail to effect formation of aecia, but that cross-relations between members of two mating types are fertile.

It appears that only two mating types have thus far been identified in the tests that have been made in those rust fungi that exhibit *bisexual heterothallism.* This indicates a haploid genetic control by only one allelic pair of factors, in which case the constitution of the diploid nucleus in the life cycle of all individuals consists of *only one genotype.* This condition cannot exist in diploid flowering plants or in animals that have incompatibilities.

Bisexual heterothallism versus unisexual heterothallism. As recently as 1941, Buller (1941) listed *Puccinia graminis* (and also *Coprinus lagopus*) as heterothallic and as having "the sex separated one from the other in different haploid mycelia." According to this view the mating would be unisexual heterothallism. Buller failed to consider that the haplophase of *Puccina graminis* is actually bisexual and that incompatibilities which are superimposed on sexual differentiations effect self- and intra-mating group cross-incompatibilities. That this is the condition has been recognized by Jackson (1944) who stated that the mycelia of *Puccinia graminis* and of certain other bisexual heterothallic fungi are not "thalli of opposite sex" but are actually "bisexual (hermaphroditic) self-sterile, and inter-fertile." It may be emphasized that there are also cross-incompatibilities among the members of each mating group.

3. BIPOLAR INCOMPATIBILITIES IN ASCOMYCETES

Recent studies, summarized by Jackson (1944), have demonstrated "the widespread occurrence of a sperma-

tial (microconidial) type of sexuality in the Ascomycetes.'' The information also definitely indicates widespread bisexuality and bipolar incompatibilities among many cases of so-called ''heterothallism.'' In such cases there is segregation of the *S* factors in meiosis and for the sexuality of nuclei there are somatic differentiations. The expressions of sexuality, especially of nuclei, are masked by (a) the multinucleated condition of both haplont and dikaryont mycelia, (b) by the loose dikaryotic association of nuclei during a period of extended vegetative activity, (c) by diversities in the extent of nuclear migrations, and (d) by the reversibility of nuclear sexuality.

In *Sclerotinia Gladioli* Drayton (1934) reported that a mycelium is a bisexual haplont which produces both spermatia and receptive trichogynes. But there is bipolar mating which involves self-incompatibilities, intra-mating group cross-incompatibilities and inter-group fertility. In this obligate parasite there is a short life cycle with the dikaryotic association limited to a few generations of ascogenous hyphae.

Hermaphroditism in dikaryotic ascospores. In certain species such as *Pleurage anserina* (Ames, 1932, 1934) and *Neurospora tetrasperma* (Dodge, 1928, 1936, 1942) the mechanism of ascospore formation provides each of the four ascospores in an ascus with two nuclei. Since a mycelium from such a spore is sexually self-reproducing it has generally been considered that these two nuclei are of opposite sex, male and female, and that it is their nuclear offspring that finally fuse. That the sex differentiation of these nuclei is not a definite and irreversible segregation has been shown by the following method. A nucleus may be isolated either in uninucleated ascospores or in uninucleated conidia. When a mycelium is grown from such a spore it will produce both spermatia and trichogyne-like structures and hence is a functional hermaphrodite. But such an individual mycelium is self-incompatible and a number of them exhibit bipolar mating incompatibilities. Thus the nuclear sexuality in the

binucleated ascospore is reversible but the incompatibility factor remains constant. The incompatible reactions of the mycelium in mating should not be confused with nuclear reactions and with the nuclear sexuality of dikaryotic association, of pairing in ascogonous hyphae and finally of their fusion in the ascus. The two are quite different aspects of sexual reproduction. The binucleated dikaryotic ascospore is actually a double hermaphrodite with nuclear sex differentiation a matter of differentiation. Dodge has repeatedly called the mycelia that grow from these uninucleated spores "unisexual" solely because they do not produce perithecia unless mated. Ames very definitely recognizes that the uninucleated mycelia are hermaphrodites and that the failures in mating involve "self-sterility" factors.

Bipolar incompatibilities in Neurospora sitophila and in related species that have uninucleated ascospores have repeatedly been referred to by Dodge and by Buller as the mating of mycelia of opposite sexes. But Dodge (1939) states that "every mycelium of *Neurospora sitophila* develops (1) incipient ascocarps with receptive organs, (2) small microconidia and spermatia, and (3) large monilioid conidia." Hence each monosporous mycelium is a functional hermaphrodite. But there is self-incompatibility and also intra-genotypic cross-incompatibility. In the inter-genotypic mating there are fusions of mycelia and also spermatial and conidial cross-fertilizations. The incompatibility factors segregate in meiosis and effect bisexual heterothallism, but nuclear sexuality is a matter of somatic differentiation.

In *Hypomyces solani cucurbitae*. Hansen and Snyder (1943) have reported the operation of incompatibility factors in the matings between hermaphroditic mycelia and unisexual male mycelia that have evidently been derived from hermaphrodites by mutation. The self-incompatible bisexual mycelia comprise two mating groups that are intra-incompatible but inter-fertile (S_1 and S_2). But the male mycelia also comprise two mating

groups. When a bisexual S_1 is mated with a male S_1, or a bisexual S_2 is mated with a male S_2 there is incompatibility. When a bisexual S_1 is mated with a male S_2, or a bisexual S_2 is mated with a male S_1 only the bisexuals produce perithecia. In these tests the hermaphroditic mycelia "are grown to maturity and have receptive perithecial primordia," and then the transfer of "any part of the living thallus, ascospores, conidia, or bits of mycelium can act as the male fertilizing agent" provided there is an inter-group relationship. The inability of the male mycelia to form perithecial primordia and to receive nuclei from hermaphrodites are, it would seem, adequate criteria of unisexual maleness. Hansen and Snyder note that sex and incompatibility are distinct and independent characters.

Concluding remarks regarding the fungi. In the fungi more critical studies and evaluations are needed to distinguish (1) the species whose members are able to function only as one sex, (2) the species whose members are bisexual and able to function in self-reproduction or in unrestricted intraspecific relations, and (3) those that are bisexual but whose intraspecific reproduction is limited by incompatibilities. Much further data are needed before an adequate evaluation can be made of the scope and role of the processes of cross-reproduction between bisexual mycelia which possess no incompatibilities. Homothallic reproduction may indeed be less obligatory than is usually assumed. It would seem that self-reproduction and unlimited intraspecific reproduction between sexes and sex elements must be a fundamental feature that precedes in evolutionary development the superimposed limitations of incompatibilities.

III. Diplont-Diplont Intraspecific Incompatibilities in Ciliate Protozoa

The discovery of selective reproduction and mating types in the diploid hermaphroditic species *Paramecium aurelia* was reported by Sonneborn (1937). For many

years various students of this genus believed that any one individual of a species could mate with any other one, exchange nuclei, separate, and then continue in vegetative vigor and fission multiplication until the next mating period. This was frequently called "sexless reproduction," chiefly because there were often no morphological differences in the conjugants, but also because the two individuals are hermaphrodites. Zoologists have frequently insisted that there is no sex in hermaphrodites; meaning that in them there is no unisexualism such as is general in animals.

Investigations of other species and genera of ciliates soon followed (Jennings, Sonneborn, Kimball, and others) which revealed considerable diversity in the number and the behavior of the mating groups. But it appears that intraspecific incompatibilities, comparable in the most important features to those already discussed, are frequent if not the rule in the genus *Paramecium* and in related genera.

The most important of the nuclear processes in sexual reproduction in these unicellular animals are believed to be chiefly as follows:—Each conjugant is a complete animal which has at least one generative nucleus that is diploid at the time of mating. Hence the mating is a diplont-diplont reaction.

After conjugation begins there is meiosis in which only one haploid nucleus survives. This undergoes *mitotic division* and the two sister nuclei become differentiated in sex-behavior though identical in constitution. One nucleus remains in its cytoplasm; one migrates into the cytoplasmic body of the other conjugant. This formation of two differentiated nuclei is the first expression of nuclear sexuality. Then there is the mutual exchange of what we may call male gametes. This effects reciprocal cross-fertilization between members of two mating groups within each of which there is cross-incompatibility.

Certain features of this conjugation are similar to

those in various of the fungi. In the fungi there is conjugation between cells of the haploid bisexual mycelia. In both there is somatic sexual differentiation of two sister nuclei with exchange and mutual cross-fertilization. In both the incompatibilities inhibit certain conjugations. In the fungi the reactions are haploid-haploid; in the ciliates they are diploid-diploid.

Bipolar incompatibilities in P. aurelia. Sonneborn (1927) found that the population of each of four different intersterile varieties of *P. aurelia* comprise only two mating types. At first these were called for convenience "sex I and sex II" but soon the designation was changed to "mating types" and "caryonides" for it was definitely recognized that all the individuals "are functionally hermaphroditic, each conjugant of a pair fertilizing the other one" (Sonneborn, 1938). Thus it was recognized that evaluations in terms of reactions between *two sexes* are inadequate. It is to be noted that in this case the different races of the one species exhibit the specificity barrier to hybridization equal to that between species that will not hybridize.

Multiple incompatibilities. More complicated mating systems were reported in *Paramecium busaria* by Jennings (1938 and 1939) and numerous researches by him have been reported since that date. Three varieties were identified; these were intersterile, due it appears to varietal specificity and not to incompatibilities. Four mating types were recognized in each of two varieties but the other variety comprised eight mating groups. The members of each group did not mate with each other, but any one of any group would mate with any one of any other group of the same variety. There was no intergroup incompatibility.

Genetical analyses of the progenies of a mating have proven difficult even for the populations that have two and four mating groups. For example, the data available indicate that at least three of the four mating types will give segregations of all four types. Jennings (1942)

recognizes that such genetic behavior is not to be analyzed in terms of two allelic series ($S_1S_2Z_1Z_2$ or $AaBb$) of two factors each and he states that "it appears best to await further knowledge before speculating more on the mechanism of the inheritance." Genetical analysis of progenies in the species of *Paramecium* (*P. aurelia* and *P. busaria*) is somewhat difficult for there are complicated internal processes involving nuclear reorganizations of endomixis and autogamy, endo-self-reproduction, and self-differentiation or change of mating type (Jennings, 1941). Further factoral genetic analyses await more definite data on these conditions and processes in relation to the segregations in progenies. These complications are being studied and the results obtained to date have been reported and discussed especially by Jennings, Sonneborn and Kimball.

Incompatibilities in Euplotes patella. In the studies of another ciliate, *Euplotes patella,* Kimball (1943) found no complications of endo-self-reproduction and self-differentiation and hence he was able to analyze the six intra-incompatible but cross-fertile mating groups in terms of "mating type" factors.

In comparison to incompatibilities in bisexual diploid flowering plants there is intra-genotypic cross-incompatibility but complete inter-genotypic cross-fertility.

In Kimball's interpretation there are only three S factors (Kimball's mating type factors) in one allelic series. The diploid combinations give three heterozygotes (S_1S_2; S_1S_3; S_2S_3) and three homozygous genotypes (S_1S_1; S_2S_2; S_3S_3). This genetic pattern is like that assumed for the simplest personate incompatibilities in flowering plants except that these reactions are diplont-diplont with each conjugant possessing two S factors. Hence the reactions within each conjugant and between them involve relative activities of two factors. There is no opportunity for hidden incompatibility or for the elimination of homozygotes. Although homozygotes occur they are normally not self- or intra-reproducing. The occurrence

of homozygotes emphasizes the fact that the incompatibilities are exclusively inhibitions of the conjugation mechanism and are independent of gametic reactions.

The nature of incompatibilities in ciliates. There is not time to-day to review the numerous excellent studies by Jennings, Sonneborn, Kimball and others on various phases of the life cycles and on the features and processes involved in sexual reproduction of the ciliates. It is, however, obvious that incompatibilities inhibit certain matings, particularly those that are intra-genotypic. Thus far it appears that the evaluations of the various investigators consider that the action of the mating factors effect both the successful matings and the failures in mating. It may be suggested that the mating reactions constitute a fundamental feature of intra-specific sexual reproduction and that the incompatibilities are superimposed as modifying factors which effect only the incompatible reactions.

Jennings (1939, page 430) has noted that, in respect (a) to "self-sterility" and intra-group cross-sterility which effect failures in reproduction and (b) to successful inter-group mating which effect reproduction, there is similarity and possible relationship between the "self-sterility" of flowering plants and the so-called "sexuality" of the infusaria.

IV. Concluding Remarks

1. The present knowledge regarding the extent of intraspecific incompatibilities in the vast array of plants and animals is relatively meagre yet it is sufficiently complete for certain of the species in which it is known to provide a basis for the recognition of the fundamental features.

2. The incompatibilities noted in this presentation are selective limitations to the sexual reproduction of homomorphic hermaphrodites. They limit or prevent both self-reproduction and intra-genotypic cross-reproduction. They effect inter-genotypic intraspecific reproduction.

3. Incompatibilities operate by inhibiting certain of the physiological interactions that are essential to sexual reproduction but which are not features of nuclear or gametic sexuality.

4. Pollen-tube reactions in the pistils of flowering plants, fusions of mycelia and spermatial fertilizations in fungi, and conjugations between individuals of ciliates are all stabilized reactions of intraspecific sexual reproduction. When there are no incompatibilities there is unrestricted interaction in these features of intraspecific reproduction. Incompatibilities are superimposed on these mechanisms and they effect certain failures in interactions which would otherwise occur.

5. Incompatibilities are genetically determined by factors which segregate in meiosis. In the homomorphic bisexual members of a population they may be the only feature of sexuality that does segregate in meiosis. This situation has not been recognized in many considerations of sexuality especially in the fungi.

6. The simplest mode of incompatibilities is that which is determined by a single allelic pair of factors (personate mode) operating in haplont-haplont relations. Then there may be only two mating groups. A minimum number of multiple alleles in a haplont-diplont relation is three. In all the classes there may be numerous multiple factors and numerous mating genotypes. Further complexities involve two or more allelic series (a) of incompatibility factors (amphipersonate) or (b) of one such series in complementary relations with factors which favor fertility (associate mode) or of more than one series of each (amphiassociate).

7. The basic incompatibility reaction is evidently one of independent self-antagonism. But the presence of two or more different factors enforces various types of complementary and competitive reactions.

8. In addition to incompatibilities there are other methods of preventing self-and intra-genotypic reproduction and of enforcing bigenotypic reproduction in hermaphro-

dites. (a) There are herkogamy and dichogamy which operate to separate elements of sexual reproduction previous to their interaction. (b) There are the conditions of polymorphism, especially developed in dimorphic and trimorphic species of flowering plants, in which incompatible reactions are correlated with morphological features.

It is of course to be recognized that in any truly dioecious species the reproduction of the unisexual individuals is obligately bigenotypic.

9. Intraspecific incompatibilities operate with remarkable similarity in phanerogams, in fungi, and in ciliates. Differences in the locus of sexual reproduction in the life cycles of these diverse and phylogenetically widely separated groups of organisms are reflected in three distinct classes of expression and genetic control which may be designated (I) haplont-diplont, (II) haplont-haplont, and (III) diplont-diplont. Without doubt future studies in the groups mentioned and in other groups of plants and animals that were not mentioned will reveal further modes or even other classes of reaction and determination.

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A COMPLEMENTARY LETHAL EFFECT IN THE SEX-LINKED GROUP OF HABROBRACON[1]

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ACCORDING to the multiple allele theory of sex determination in the parasitic wasp *Habrobracon juglandis* (Ashmead) a single series of allelic factors, designated the x series, differentiates sex (Bostian, 1939, Horn, 1943, Whiting, 1940, 1943). A haploid male may contain any one of the *n* members of this series—xa, xb, xc, etc.; a diploid male is homozygous—xa/xa, xb/xb, xc/xc, etc.; and a female may have any one of the $\frac{n^2-n}{2}$ possible heterozygous combinations—xa/xb, xa/xc, xb/xc, etc.

These alleles, regarded as chromosome segments containing many genes, nevertheless act as units in heredity, indicating lack of crossing over within the segment. Crossing over occurs between the x alleles and various mutant genes both to the left and to the right.

No experimental proof for the multiple genic nature of the x alleles has yet been obtained. It is tentatively assumed as being more probable than a series of single genes because of the complexity of sex differences and because sex in Drosophila and in other forms is differentiated by many genes segregating as a unit (X *vs.* Y).

About one third of the offspring of a mated female are haploid males from unfertilized eggs. If the sex allele of the father (xc) differs from those of the mother (xa/xb), the zygous offspring are all females (xa/xc and xb/xc) constituting a three-allele fraternity. If, however, the father has a sex allele (xa) similar to one of those possessed by the mother (xa/xb), the zygous offspring are

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females (xa/xb) and diploid males (xa/xa) constituting a two-allele fraternity. Diploid males are of low viability relative to their sisters, so that a 1:1 ratio is not to be expected and there are many nonhatchable eggs.

Allelism of the series of sex-differentiating factors was shown by their linkage with the mutant gene fused, *fu,* affecting antennae, tarsi, wings. In two-allele fraternities from mothers heterozygous for fused crossed with fused males, about ten per cent. of the females and about ninety per cent. of the diploid males are fused $\left(\frac{xa\ +}{xb\ fu}\right.$ female by $\underline{xb\ fu}$ male produces 90 per cent. $\frac{xa\ +}{xb\ fu}$, 10 per cent. $\frac{xa\ fu}{xb\ fu}$, 90 per cent. $\frac{xb\ fu}{xb\ fu}$, 10 per cent. $\left.\frac{xb\ +}{xb\ fu}\right)$, or about 90 per cent. of the females and about 10 per cent. of the diploid males are fused $\left(\frac{xa\ +}{xb\ fu}\right.$ female by $\underline{xa\ fu}$ male produces 90 per cent. $\frac{xb\ fu}{xa\ fu}$, 10 per cent. $\frac{xb\ +}{xa\ fu}$, 90 per cent. $\frac{xa\ +}{xa\ fu}$, 10 per cent. $\left.\frac{xa\ fu}{xa\ fu}\right)$ according as fused is associated with the same sex allele or with opposite alleles in the parents. This rule has been shown to apply for five inbred stocks involving nine different alleles—xa/xb, xc/xd, xe/xf, xg/xh, xa/xi (Whiting, 1943).

In three-allele fraternities sex-linkage of fused is masked because the two genotypically different types of females (xa/xc and xb/xc) are indistinguishable. Fused and non-fused females appear in approximately equal numbers and there are no diploid males.

Horn (1943) made reciprocal crosses between two stocks having different sex alleles (xa/xb and xe/xf). The males were in each case fused. F_2 fused males were backcrossed to females of both parental stocks heterozygous for fused. Each of these F_2 fused males proved to have a sex differentiator from one parental stock only, usually the paternal because the gene fused was of pater-

nal origin. All Horn's data were according to expectation.

The investigation reported in the present paper was originally planned to test the multiple allele theory further by backcrossing the F_1 hybrid females from two stocks with different sex alleles (xa/xb and xc/xd) to males of one of the parent stocks (xa/xb). The initial experiment indicated what appeared to be a lethal effect on certain classes of the offspring from the backcross and it seemed desirable to investigate the nature and location of the lethal factor further as a contribution toward the general problem of genetics in Habrobracon.

Materials and Methods

In addition to fused, the gene stubby, reducing number of antennal segments, was used in the experiments because it had been shown to be sex-linked. Hager (1941) showed linkage of fused with stubby and loose linkage of stubby with sex (33.6 to 37.5 per cent. recombinations). He arranged the factors with intervals as follows: x—(8.6 to 17.6)—*fu*—(22 to 24.2)—*sb*.

Sex alleles and origins of the six stocks used in these experiments have been reported (Whiting, 1943). Fused is kept in heterozygous condition because of female-sterility. Formulae of the stock females, including orange eye color, *o,* stubby antennae, *sb,* and fused antennae, *fu,* as well as sex alleles are as follows:

(1) $\frac{\text{o xc}}{\text{o xd}}$ (11–o) (2) $\frac{\text{xa sb}}{\text{xb sb}}$ (35–sb) (3) $\frac{\text{o xa sb}}{\text{o xb sb}}$

(4) $\frac{\text{o xe}}{\text{o xf}}$ (5) $\frac{\text{xa +}}{\text{xb fu}}$ (6) $\frac{\text{o xa +}}{\text{o xb fu}}$

In the experiments orange-eyed females heterozygous for stubby (or for fused) were crossed to black-eyed stubby (or fused) males. Thus the diploid biparental sons could be separated by their black eyes from their haploid orange-eyed brothers.

All progeny which did not emerge from pupal cases were removed with a needle and were classified whenever possible. Eye color, as well as the traits fused and stubby, is separable in all but the youngest pupae.

EXPERIMENTS WITH STUBBY ANTENNAE

Experiment 1. Orange stubby females, $\frac{o\ xa\ sb}{o\ xb\ sb}$, were mated to orange males, $\underline{o}\ \underline{xc}$ or $\underline{o}\ \underline{xd}$. The daughters, designated "F_1 mothers" below, were mated to black-eyed stubby males, $\underline{xa\ sb}$ or $\underline{xb\ sb}$, designated "Fathers" below. Two-allele and three-allele fraternities are to be expected in equal numbers as shown below.

F_1 mothers	*Fathers* $\underline{xa\ sb}$	$\underline{xb\ sb}$
$\frac{o\ xa\ sb}{o\ xc\ +}$	two-allele	three-allele
$\frac{o\ xa\ sb}{o\ xd\ +}$	two-allele	three-allele
$\frac{o\ xb\ sb}{o\ xc\ +}$	three-allele	two-allele
$\frac{o\ xb\ sb}{o\ xd\ +}$	three-allele	two-allele

In the three-allele fraternities sex-linkage of stubby is masked, as in the case of fused, because the two genotypes of females are indistinguishable. In the two-allele fraternities a deficiency of stubby females (35 per cent.) is to be expected because they are crossovers, but stubby should be in excess (65 per cent.) among the diploid males because they represent the original combination.

Since the results obtained in the first tests under this experiment proved contrary to expectation, they were repeated twice, the first repetition closely following the original, the second a year later. Different strains of the same stock were used. All agreed in showing a deficiency of wild type offspring.

In the 68 fraternities without diploid males, the females were 2,101 stubby, 1,147 wild type; the haploid males were 374 orange stubby, 469 orange. In the 39 fraternities including diploid males, the females were 482 stubby, 493 wild type; the diploid males were 191 stubby, 49 wild type; the haploid males were 229 orange stubby, 286 orange. Average number of females per fraternity without diploid males was therefore 47.7, but only 25.0 when diploid males were present. Ratio of females to haploid

males was 3.85 in the former group, but only 1.89 in the latter. These results are to be expected since only half of the fertilized eggs in two-allele crosses are female-producing.

Studies on hatchability of eggs and viability of offspring (Bostian, 1935) have shown greater fecundity in three-allele than in two-allele crosses. Comparable results are also obtained without observation of eggs by using number of egg-laying days (total days of active adult lives of mothers kept in incubators) as a basis of comparison. In Experiment 1 there were 3,248 females produced in 1,044 egg-laying days (3.11 per day) by mothers with no diploid sons and 975 females in 635 egg-laying days (1.535 per day) by mothers with diploid sons.

Comparison may be made between the three-allele crosses of this experiment and certain other crosses between stocks with different sex alleles (*o/o xc/xd* by *xa sb* or *xb sb*) which produced 483 females in 135 egg-laying days (3.57 per day). Although differences in cultural conditions may have influenced the result, the fact that the three-allele fraternities of the experiment averaged fewer females suggests the presence of a lethal.

Experiment 2. This experiment was similar to Experiment 1 except that the F_1 mothers resulted from the reciprocal cross. The daughters of orange females, $\frac{o\ xc}{o\ xd}$ by orange stubby males, $\underline{o}\ \underline{xa\ sb}$ or $\underline{o}\ \underline{xb\ sb}$, were mated to black-eyed stubby males, $\underline{xa\ sb}$ or $\underline{xb\ sb}$. Of the two tests in this experiment, the second, made after the lapse of a year, agreed with the first in results obtained.

In the 15 fraternities without diploid males, females were 454 stubby, 276 wild type; haploid males were 121 orange stubby, 125 orange. In the 15 fraternities including diploid males, females were 142 stubby, 152 wild type; diploid males were 47 stubby, 9 wild type. In this group counts of haploid males can not be used because of presence of the gene fused reducing viability. Among the diploid offspring in this experiment also, there is a marked deficiency of wild type offspring. Females lack-

ing diploid brothers average 48.7 per fraternity, but only 19.6 per fraternity as expected when diploid males are present.

Experiment 3. This experiment was similar to Experiment 2 except that $\frac{o}{o}\frac{xe}{xf}$ females were used instead of $\frac{o}{o}\frac{xc}{xd}$ females. The daughters of orange females, $\frac{o}{o}\frac{xe}{xf}$, by orange stubby males, $\underline{o\ xa\ sb}$ or $\underline{o\ xb\ sb}$, were mated to black-eyed stubby males, $\underline{xa\ sb}$ or $\underline{xb\ sb}$. Twenty matings were made of which 15 failed to produce diploid males. Since numbers of offspring were rather small, it is probable that some of these 15 involved only two alleles and that diploid males were lacking due to error of sampling.

In the 15 fraternities without diploid males, the females were 316 stubby, 215 wild type; the haploid males were 122 orange stubby, 178 orange. In the five fraternities including diploid males, the females were 47 stubby, 46 wild type; the diploid males were 18 stubby, 2 wild type; the haploid males were 41 orange stubby, 58 orange.

In the former group there are 35.4 females per fraternity, in the latter only 18.6. Ratio of females to haploid males is 1.77 in the former, but only 0.94 in the latter as expected. The ratio of wild type to stubby females is low in this experiment, indicating that the lethal is present in xe/xf material as in xc/xd. In the five fraternities including diploid males, only about half of the females are wild type, instead of the 65 per cent. expected on the basis of 35 per cent. crossing over between stubby and x. In the 15 fraternities without diploid males, stubby females are more numerous than wild type, 1.47 : 1 instead of 1 : 1.

For Experiments 1, 2 and 3, in the fraternities lacking diploid males, ratios of stubby to wild type females are 1.83 : 1, 1.64 : 1 and 1.47 : 1, respectively. Since some of these fraternities in Experiment 3 were probably two-allele, the data are not used in the calculations below.

It is probable that all or nearly all the 83 fraternities of Experiments 1 and 2 lacking diploid males were three-

allele because numbers were larger. The fact that wild type were reduced in Experiment 1 even more than in Experiment 2 indicates that no two-allele fraternities were included despite the fact that there were more fraternities lacking (68) than including (39) diploid males. Females in these two experiments totalled 2,555 stubby, and 1,423 wild type, giving a ratio of 1.8 : 1 for the three-allele fraternities, instead of the expected 1 : 1. A lethal factor linked with the dominant allele to stubby would therefore allow 36 per cent. crossovers if its action were completely lethal.

In Experiments 1, 2 and 3, ratios of stubby to wild type among the females of the fraternities including diploid males (two-allele) are similar. In the total of 59 fraternities females were 671 stubby, 691 wild type; diploid males were 256 stubby, 60 wild type.

If it be assumed that the factor or set of factors decreasing wild type diploids is similarly effective in the diploid males and females of the two-allele fraternities and in the females of the three-allele fraternities, the crossover value between x and stubby may be found. As stated above the ratio of stubby to wild type females in the three-allele fraternities is 1.8 : 1 instead of 1 : 1. The expected number of wild type females and males in the two-allele fraternities may therefore be obtained by multiplying the actual number by 1.8. This gives 1243.8 *vs.* 691 for the females and 108.0 *vs.* 60 for the males. Crossing over as shown by the females is then 35.1 per cent. and by the diploid males 29.6 per cent. The former value is within the range of variations found in experiments not involving a lethal (Hager, 1941). The deviation of the latter is insignificant.

Since crossing over seems to be closely similar between x and *sb* and between the lethal and *sb*, it would be expected that x and the lethal would be closely linked if the latter lies to the left of *sb*. This would very greatly decrease the number of females. Moreover, among the females, the ratio of stubby to wild type or of wild type

to stubby should be similar to the ratio of stubby to wild type among the diploid males, according as the lethal were to the right or to the left of x respectively. These conditions are far from being met.

Experiment with Fused

Experiment 4 was planned as a further test of the position of the lethal. Orange females, $\frac{o\ xc}{o\ xd}$, were mated to orange fused males, $\underline{o}\ \underline{xa\ fu}$ or $\underline{o}\ \underline{xb\ fu}$. The daughters, designated "F_1 mothers" below, were mated to black-eyed fused males, $\underline{xa\ fu}$ or $\underline{xb\ fu}$, designated "Fathers" below. Two-allele and three-allele fraternities are to be expected as when stubby was used. The various combinations are shown below.

F_1 mothers	*Fathers* $\underline{xa\ fu}$	*Fathers* $\underline{xb\ fu}$
$\frac{o\ xc\ +}{o\ xa\ fu}$	two-allele	three-allele
$\frac{o\ xc\ +}{o\ xb\ fu}$	three-allele	two-allele
$\frac{o\ xd\ +}{o\ xa\ fu}$	two-allele	three-allele
$\frac{o\ xd\ +}{o\ xb\ fu}$	three-allele	two-allele

Because of sex-linkage and female-sterility of fused and recent derivation of the orange fused stock from the fused stock, it may be supposed that association of fused occurred more frequently with the same sex allele in the F_1 mothers and fathers. Two-allele fraternities may therefore be expected to occur more often than three-allele. There were actually 46 of the former type but only six of the latter.

In the six three-allele fraternities of this experiment, the females were 293 fused, 332 wild type; the haploid males were 120 orange fused, 128 orange. This is close to the 1:1 ratio expected for fused if its somewhat lowered viability be considered.

In the 46 two-allele fraternities, the females were 396 fused, 2,655 wild type; the diploid males were 650 fused,

41 wild type; the haploid males were 1,108 orange fused, 1,110 orange, giving crossover values 12.98 per cent. as shown by the females and 5.93 per cent. as shown by the diploid males. As expected females are almost twice as frequent in the three-allele fraternities as in the two-allele, ratio of females to haploid males being 2.12 among the former, 1.37 among the latter.

In this experiment there is evidently no appreciable effect of the lethal which must therefore be located to the right of stubby.

Semilethals and the Linkage Map

Table 1 shows the various combinations expected from a cross of an orange-eyed female heterozygous for stubby and for a pair of complementary lethal factors, L^a/L^b, by a stubby male having one of these factors, L^b. Stubby is associated with the same sex factor, xa, in the female as in the male. The alternative gametic types of eggs combined with the single type of sperm are shown in the second column for the noncrossovers, for the single crossovers in regions 1 and 2 and for the doubles respectively. The third column shows the distribution of the four phenotypes with λ designating the heterozygous combination L^a/L^b. Actual numbers of offspring are shown in the fourth column followed by the ratios of stubby and wild type given separately for the females and for the diploid males.

The ratio of the phenotypes depends upon three things: (1) degree of lethality assigned to L^a/L^b, (2) sex, diploid males being less viable than females, and (3) crossing over and interference, which determine the ratio of genotypes.

In the three-allele crosses of Experiments 1 and 2, the eggs will of course be comparable in type and ratio to those in Table 1, but since the sperm have a different sex factor all zygotes will be female-producing. Only stubby and the lethal will have a perceptible effect.

Following the actual ratios of offspring in Table 1, theoretical ratios are shown calculated on the basis of

TABLE 1

Results from Crossing Orange-eyed Females (o/o xc/xa) Heterozygous for Stubby Antennae (sb) and for a Pair of Complementary Lethal Factors (L^a/L^b) with Black-eyed (+) Stubby Males Having a Similar Sex Allele (xa). Actual Numbers and Ratios of Wild Type and Stubby Daughters and Sons Are Shown and Theoretical Ratios Based on Three-allele Crosses if L^a/L^b Is Assumed to be Either Completely Lethal or Semilethal

Mother $\frac{\text{o xc} \quad + \quad L^a}{\text{o xa } -0.35- \text{ sb } -?- \; L^b}$ — Father $\underline{+}\ \underline{\text{xa sb } L^b}$

Crossover regions	Zygotes eggs/sperm	Phenotypes of offspring	Actual numbers	Ratios ♀♀	Ratios ♂♂	Theoretical ratios of offspring: L^a/L^b inviable, Region 2—0.36: Total	♀♀	♂♂	L^a/L^b 0.481 viable, Region 2—0.10: Total	♀♀	♂♂
(–)	$\frac{\text{o xc} + L^a}{+ \text{ xa sb } L^b}$	+ ♀ λ				0			0.282	0.415	
	$\frac{\text{o xa sb } L^b}{+ \text{ xa sb } L^b}$	sb ♂	256		0.810	0.416		0.767	0.585		0.728
(1)	$\frac{\text{o xc sb } L^b}{+ \text{ xa sb } L^b}$	sb ♀	671	0.495		0.224	0.489		0.315	0.464	
	$\frac{\text{o xa} + L^a}{+ \text{ xa sb } L^b}$	+ ♂ λ				0			0.152		0.189
(2)	$\frac{\text{o xc} + L^b}{+ \text{ xa sb } L^b}$	+ ♀	691	0.507		0.234	0.511		0.065	0.096	
	$\frac{\text{o xa sb } L^a}{+ \text{ xa sb } L^b}$	sb ♂ λ				0			0.031		0.039
(1, 2)	$\frac{\text{o xc sb } L^a}{+ \text{ xa sb } L^b}$	sb ♀ λ				0			0.017	0.025	
	$\frac{\text{o xa} + L^b}{+ \text{ xa sb } L^b}$	+ ♂	60		0.190	0.126		0.233	0.035		0.044

0.35 as the recombination ratio between x and *sb*. If the combination L^a/L^b is assumed to be completely lethal, the data from the three-allele crosses give 0.36 as its recombination ratio with *sb*. With these linkage map intervals, expected ratios of stubby and wild type are calculated and given separately for females and diploid males (columns 7, 8, 9). Agreement is very close to the actual ratio in the two-allele fraternities.

These calculations made on the basis of complete inviability of the L^a/L^b genotype disregard the fact that the mothers, which are of this type, are nevertheless viable. It must therefore be assumed that the lethal effect is not complete, that L^a/L^b is semilethal.

Carson (1941), studying linkage and interference in a three-point cross of Habrobracon involving the genes broken, white and stumpy, presented evidence for a semilethal located an appreciable distance to the left of broken and acting like a recessive, killing a proportion of the sons of heterozygous virgin mothers. He states "map position of a semilethal can not be determined since the degree of lethality is unknown. As higher degrees are assumed, the factor would be shifted to the left, toward the locus of a complete lethal; as lower degrees are assumed, the factor would more closely approximate the locus of *bk*."

In Table 1, columns 10, 11, 12 give the ratios of offspring expected if region 2 is only 10 units in length and L^a/L^b is semilethal permitting viability sufficient to make the phenotypic ratio similar to that expected with region 2 thirty-six units in length and L^a/L^b inviable. To the L^b/L^b noncrossovers for region 2 have been added a proportion, p, of the L^a/L^b crossovers for region 2 of similar phenotype and to the L^b/L^b crossovers for region 2 have been added a similar proportion of the L^a/L^b noncrossovers of similar phenotype. In the present instance, p ($=0.481481$) is found from $\frac{0.90+0.10\,p}{0.10+0.90\,p}=\frac{0.64}{0.36}$. This method applies only if coincidence is 100 per cent.

Degree of lethality of a semilethal factor differs widely

under diverse environmental conditions and in different stocks. This has been shown in Habrobracon for a number of visible mutant types of low viability. The mutant genes are here semilethals which have a recognizable effect on the surviving individuals. Factors ordinarily designated as semilethals presumably differ from these only because of our failure to find a conveniently visible trait difference.

In Habrobracon with its haploid males, stocks very quickly become pure for modifying factors by lethal selection. It seems likely that thus a balance of factors should be readily attained tending toward greater viability. Relatively disharmonic combinations may be expected to enhance by their cumulative effect the influence of a semilethal among the progeny of hybrid females. A larger proportion of the L^a/L^b daughters than of the L^a/L^b sisters of the hybrid mother might then be inviable.

Complementary Lethals in Other Forms

Complementary lethal effects are found in many hybrid embryos resulting from species crosses. Syngamy and cleavage mitoses may be normal, but disharmonic developmental processes occurring later result in death. Complementary lethals are also noted in intervarietal crosses and in certain instances the factorial basis has here been analyzed. Thus Wiebe (1934) has shown that F_1 seeds resulting from crosses of two barley varieties germinate normally but the hybrid embryo usually fails to emerge or the plumule dies. The F_1 generation from crosses of certain wheat varieties likewise is inviable (Caldwell and Compton, 1943, Heyne, Wiebe, Painter, 1943) but here the hybrid plants develop normally to the two-leaf stage. Progressive necrosis of the leaves then takes place resulting in death. Both in barley and in wheat it was shown by crossing to other varieties and subsequent crossing of the offspring that the lethal section was caused by the presence of the dominant alleles of two independently segregating pairs. Neither dominant alone, whether homozygous or heterozygous, was lethal. Other heredi-

tary factors occur in wheat causing necrosis which is nonlethal to the plant or semilethal.

Sears (1944) has shown complementary lethal effects in intergeneric hybrids involving Triticum. A single-factor difference may exist between two varieties of a species with one allele determining inviability in the generic cross, but there may be "several factors from each species, all necessary for inviability of the hybrid."

In *Drosophila melanogaster* Schultz (1929) has shown complementary lethal and semilethal effects in the combination of certain Minutes with different Delta alleles and with Jammed. Muller (1940, p. 196) states "It is so common an experience as not to occasion any remark to find that two or more mutant genes, whose viability is not noticeably low when in separate stocks, give a stock whose viability is very much reduced—more than additively—when in combination."

In the example under consideration in Habrobracon, the factor L^a may be represented as two closely linked elements, L_1 l_2, a dominant and a recessive, while L^b contains the alternatives, l_1 L_2. No effect takes place in the azygous male or in the homozygous male or female, but in the heterozygote the cumulative effect of the two dominants, supplemented by modifying factors segregating in oogenesis of the mother, results in disharmonic development with lethal threshold.

Summary

In five tests involving reciprocal crosses of two orange-eyed stocks and in one test of one of these stocks having the loosely sex-linked gene stubby with a third stock, lethal effects were present associated with the dominant allele to stubby. The F_1 females were crossed with black-eyed stubby males closely related to the orange stubby parental stock. In all cases there occurred a marked deficiency of the wild type diploid offspring, both among the males and among their sisters as well as among the females of the fraternities involving three sex-alleles in which there are no diploid males. Since no corresponding

decrease occurred among the non-stubby haploid males and since the stocks were apparently breeding true for the "lethal" factors involved, the lethal effect is regarded as complementary.

Failure of association of the lethal with sex was shown in the fraternities involving two sex alleles in which the zygous offspring are differentiated into males and females. Moreover a test similar to those involving stubby but made with the closely sex-linked gene fused in a closely related stock failed to show any lethal effect. It is then probable that the lethal factor lies to the right of stubby.

Thirty-six per cent. recombination between stubby and the lethal would occur in case of complete inviability. With about 50 per cent. viability, recombinations would be 10 per cent. Semilethality is assumed, fluctuating because of multiple factors which segregate in oogenesis of the hybrid females.

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CURRENT CONCEPTS OF PLAY IN ANIMALS

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PRESENT-DAY understanding of animal play is regrettably limited, and current views on the subject are considerably confused. On the one hand, there are the hundreds of observations made by naturalists, by animal breeders and by nearly every one who has kept a household pet to indicate that animals of many species do exhibit various types of behavior which, if they were observed in humans, would undoubtedly be called play. On the other hand stands our undeniable ignorance as to the essential nature of play, its causes and its results. The richness of the observational evidence is in sharp contrast to the poverty of scientific knowledge.

It is significant that authors of several recent American text-books on comparative or physiological psychology have failed to make any mention of play in animals, or have skipped over the subject as lightly as possible (Warden, Jenkins and Warner, 1936; Maier and Schneirla, 1935; C. T. Morgan, 1943). Their reluctance or inability to treat the topic undoubtedly derives from the exclusively observational character of available data and the obvious inadequacy of existing interpretations.

It is not the purpose of this paper to present new data pertinent to the problem under consideration, or to propose any original, all-inclusive theoretical interpretation. Instead it is hoped that a survey of existing knowledge and an evaluation of the theories presently available may point the way toward profitable lines of future work which will lead to a more complete understanding of the subject.

COMMONLY ACCEPTED CHARACTERISTICS OF PLAY

Play is generally regarded as differing from non-playful activities in several ways. Whether or not it is possible to discern any pervasive characteristics common to all forms of behavior which are commonly listed under this rubric depends upon the definition of play. At this

point, however, we shall overlook this source of difficulty and list the outstanding characteristics of playful behavior as set forth by most students of the subject.

(1) It is commonly stated or implied, although it can not be objectively demonstrated, that playful behavior in animals as in man carries an emotional element of pleasure. Not all pleasant activities are playful; but all play is assumed to be pleasurable. (2) Play is usually regarded as characteristic of the immature animal rather than the adult. Grown individuals may play; but they do so less frequently than juvenile members of their species. (3) It is usually supposed that play differs from non-playful responses in having no relatively immediate biological result which affects the continued existence of the individual or the species. In other words, play is customarily regarded as non-utilitarian. (4) The outward forms of play are relatively species-specific. Dogs play in certain ways, horses in others, and apes in still others. (5) The amount, duration and diversity of play in a given species is related to its phylogenetic position. In general, play is more frequent, more variable, and occurs during a longer portion of the life span in higher animals than in lower. The play of fishes appears infrequent and stereotyped when compared with that of lower mammals; while the play of dogs is less diversified and prolonged than that of monkeys and apes.

Types of Behavior Which Have Been Called Play

A wide variety of animal responses are frequently lumped together under the general heading of play. The categories are not clear cut, but may merge insensibly one into another; and sometimes several kinds of play may be combined in an integrated series of reactions. In listing the main types of play we shall temporarily refrain from any evaluation of the validity of the classification.

General bodily activity. Many young animals display a great deal of bodily activity, chiefly of a locomotor character, in which vast amounts of energy are expended and no obviously useful result is achieved. Fishes of some

species periodically leap above the surface of the water; some birds indulge in elaborate aerial acrobatics; colts gallop about the pasture; puppies race back and forth in the yard; kittens scamper wildly across the room over the sofa and under the chair; in addition to climbing, sliding and jumping, chimpanzees execute complicated bodily actions such as turning somersaults, or revolving rapidly in pinwheel fashion while lying at full length on the ground (Kohler, 1931). Some writers regard these reactions as a form of play (Mitchell, 1912; Haigis, 1941; Gudger, 1944).

Youthful practice of adult activities. Young animals of many species exhibit various behavior patterns which also appear in the repertoire of the adult individual; but when executed during immaturity the responses are often incomplete, and seem to lack any practical outcome. Well-known examples of such behavior, which is generally interpreted as play, are the mock battles of puppies, the pursuit and capture of any small, moving object by kittens and the infantile or juvenile sex reactions of many species (Groos, 1898).

Exploration and experimentation. Responses falling in this category may range from very simple investigatory reactions to highly complex and original types of experimentation (C. L. Morgan, 1900). The tendency of young birds and mammals to peck, scratch, claw, pull and bite at objects in their environment is illustrative of the relatively simple exploratory reactions which some observers regard as play. In contrast stand the knot-tying and pole vaulting of chimpanzees, which are also examples of manipulative or experimental behavior albeit of a higher order.

Social responses. Certain inter-individual reactions which seem to lack any practical outcome are often listed as play. The "tilting matches" of young British warblers (Pycraft, 1912), "king-of-the-mountain" games of lion cubs (Cooper, 1942), "follow-the-leader" games of young monkeys (C. L. Morgan, 1900) fall in this general category.

Social play is prominent among chimpanzees according to the descriptions of Kohler (1931). He states that when several young apes were given a large sack, one crept into the container and the others pulled it about on the ground. Small chimpanzees sometimes rode pick-aback on the shoulders of older animals and then slid downward, grasping the bearer's trunk with the hind legs and walking on the ground with the hands.

The "dancing" of young apes would probably come under the heading of social play. This activity is highly variable and ranges from spinning round and round in a solo performance to participation in rather complicated group performances. Several chimpanzees may start to march single file around a post or box. Gradually their pace increases and they trot, often with emphasis upon one foot so that a primitive kind of rhythm emerges; and as they trot and stamp, the animals may wag their heads in time with the pedal rhythm. A direct quotation from Kohler will serve to illustrate the complexity and group character of the behavior.

> As the whole group were joyously trotting round a box, little Konsul stepped to one side outside the circle, drew himself up to his full height, swung his arms to and fro in time to the trotting, and each time that fat Tschego passed him, caught her a sounding smack behind.

Inter-species reactions. Although animals of one species occasionally respond to those of a foreign species in what might be regarded as a playful manner, play between species is not common. The outstanding exception to this generalization is the play which takes place between man and his pets. If one is to accept any of the characteristics or criteria of play which are accorded common usage, it must be admitted that the dog plays with his master (Russell, 1936). The animal may engage in sham hunts or battles with the man in much the same manner as with another dog. On the other hand he may with equal readiness participate in a "learned" game such as "fetch," or perform various tricks without any material reward. It is particularly significant to note that the animal may take the initiative in beginning the interspecies play, and signalize in a variety of ways his

eagerness to tease his master into a game. In similar fashion young chimpanzees play with human companions (Wolfe, 1936); and the desire to do so is so strong that opportunity to play has successfully been used as an incentive in certain learning experiments (Yerkes and Petrunkevitch, 1925).

Criteria and Causes

The majority of interpretations purporting to define or explain play are speculative in nature, deductively derived and completely untested.

Surplus energy. The poet Schiller is reputed to have suggested that play is an expression of overflowing energy which can find no other outlet. Actually, as Curti (1930) has pointed out, Schiller merely noted that playful behavior usually occurs when an ample supply of energy is available; but later writers have reinterpreted the original suggestion to form a theory stating that certain types of play constitute a release of extra physical, and perhaps mental or emotional energy.

A variation of this hypothesis, in modern dress, has been restated by Tolman (1932) in the suggestion that men and perhaps some of the lower animals have a need under certain conditions to achieve "mild harmonious fatigues." It is proposed that when the organism is in a "neutral sort of metabolic condition," and other needs or appetites are not strongly engaged, there is a condition of unspent energy. This state is regarded as one of physiological disequilibrium requiring complementary fatigue for neutralization. In defining play, Tinklepaugh (1942) states as one criterion the fact that play is a type of activity which occurs under conditions of surplus time and energy.

Suggestions of this sort have little to recommend them. In the first place they are based upon the most obvious sort of circular reasoning. The catch lies in the definition of the term "surplus." When a cat chases, catches and devours a mouse, a certain amount of energy is expended; but no one suggests that this is extra, or surplus energy. Now, when the same cat chases, catches and

chews on a rubber ball, an equal energy loss may occur; but in this case it is said to be surplus energy which has been released. Catching and eating mice is serious business for the cat (or at least the human observer thinks that it *should* be); whereas pursuit of a rubber ball serves no obvious, immediate and practical end (in so far as the observer can tell). Therefore ball chasing must be play, whereas mouse chasing is not play. Refraining for the moment from commenting upon the anthropomorphic reasoning involved, we can see that the decision as to whether or not the expended energy is surplus energy, depends upon the interpretation of the behavior as playful or serious. Therefore to set up as one criterion or explanation of play the condition that it involves the release of surplus energy is to do no more than complete the circle.

As far as mental and emotional energy are concerned, our concepts in this field are so fuzzy and debatable that it is sheer nonsense to predicate explanations of behavior upon the supposed accumulation and discharge of these hypothetical forces. Definition of one unknown in terms of a second unknown is good algebra but poor psychology.

Present-day knowledge of physiology does not support the belief that physical energy is something which can be stored up in the organism like water in a reservoir. There is no known process whereby unexpended energy "backs up" and creates a pressure, demanding release. To be sure certain sources of potential energy, such as liver glycogen, may be accumulated; but this is quite a different matter; and, thus far at least, no one has suggested that play occurs because the liver feels the need of discharging stored glycogen.

Instead of referring to energy, surplus or otherwise, it seems best to conceive of a muscle, nervous unit or organism as being either completely rested and ready to respond maximally to stimulation, or as being partially or almost completely exhausted, in need of rest and repair. Under conditions of partial or total exhaustion the organism may be expected to react weakly, incompletely, or to fail entirely to respond to stimuli from the external

environment. Such a concept would lead us to anticipate that play, which, like any other type of behavior, constitutes a response to stimulation, would occur most frequently and readily when the animal is rested and in a state of readiness to react. This is exactly what happens; but be it noted that non-playful activities also occur most frequently under the same conditions. Thus, the tired animal is less apt to play than is his rested fellow; but he is equally less likely to "work."

Several writers, including Mitchell (1912), have objected to the interpretation of playful activities as the mere discharge of a waste product; and have insisted that the energy employed in play is expended upon "the business of youth." C. L. Morgan (1900) also states that "normal" rather than "surplus" energy is involved in the play of animals.

Finally, as Groos (1898) and others have observed, superabundant energy is not always a condition of play. Young animals can often be seen to play to the point of apparent exhaustion, lie panting with fatigue, and suddenly respond to the advent of a play-inducing stimulus with the abrupt resumption of their energy-draining games.

It is generally recognized that young animals are often more active than adult members of their species (Cooper, 1942), and perhaps the observation of this difference has given illusory support to the surplus energy criterion of play.

General exuberance, or joie-de-vivre. It is often stated that playful behavior is "enjoyed for purely its own sake" (Tinklepaugh, 1942), "expresses a joy of living" or "manifests a general exuberance" (Pycraft, 1912). Some writers combine this criterion with the surplus energy criterion, and conclude that play grows out of a pleasure in being active (Haigis, 1941). From this point it is but a step to the conclusion that animals play because playing is pleasant.

Before criticizing this theory let us state unequivocably that the comparative psychologist does not look upon all animals other than man as machines which automatically

carry out their life functions without intelligence, without conscious purposes and without any emotional involvement. On the contrary, many if not all of the lower mammals, the birds, reptiles, amphibians and fishes manifest varying degrees of intelligence and adaptability. To be sure, their behavior is less variable than that of man, and their ability to profit from experience may be relatively limited; but many observers believe that the differences are more of degree than of kind. There is, furthermore, little reason to deny to animals various kinds and degrees of emotional experience. Accordingly, the most militant and objective "behaviorist" can not seriously object to the statement that the dog which romps through the snow, barking, leaping, dashing wildly hither and yon, or plays at "fetch" with his master, is enjoying the experience.

Having done our feeble best to disarm the critical reader who promptly and scornfully cries, "Mechanist!" at any one daring to speak out against anthropomorphic interpretations of animal behavior, let us proceed to examine the purported explanation of animal play as a form of activity which is engaged in solely for the pleasure it brings the performer.

The first and most obvious objection is that this so-called interpretation does not interpret nor explain. It is directly comparable to the explanations of sixteenth century theologicians who interpreted all natural phenomena as manifestations of divine will, or to the animalistic beliefs of more ancient "explainers." One might with equal accuracy state categorically that a plant grows toward the sun, a cloud moves across the sky or a stick floats on the surface of the stream, because the plant, the cloud and the stick derive pleasure from behaving as they do. Here is no explanation, no advance in the understanding of basic causal relationships responsible for the outward activity.

Explaining a playful response by referring its occurrence to one (assumed) character common to all forms of play is equivalent to explaining that water boils because it is hot. To be sure, boiling water is usually quite

hot (although its temperature may vary considerably as any tenderfoot who has tried to cook at high altitudes will ruefully attest); but the explanation for boiling is to be found in the elucidation of the relationship between the atmospheric pressure and the vapor pressure of the liquid.

Another indictment against the *joie-de-vivre* hypothesis as an explanation of animal play is that its uncritical adoption tends to discourage and render apparently unnecessary any further attempt to examine in detail the real nature of the reactions thus "explained."

Non-utilitarianism. In defining play the majority of writers have agreed that one of the criteria for this form of behavior is that it is not directly useful, although the possibility of eventually practical results is not denied. There are several practical and theoretical objections to this criterion.

Very often the conclusion that a particular act performed by an animal has no directly practical value is actually no more than a confession of the observer's ignorance. An example will illustrate this point. Various fishes, including members of the family *Belonidae,* exhibit a curious habit of "leaping" over free-floating objects such as sticks and straws. As described by Breder (1932) for *Tylosurus raphidoma* the reaction of the fish is as follows:

> First the fish will swim up slowly to the stick so as to be nearly at right angles to it (in a horizontal plane) and gently protrude the beak through the surface of the water, sliding the tip over the stick. Usually if the stick is too small and gives way too easily, or too large and gives way too little, the fish will withdraw. If it is of the proper buoyancy and sinks ever so little under the weight of the beak, a violent tail action follows and the fish clears the water, but in such a manner that usually part of the body rubs against the stick in passing and the fish falls to the other side, from which it may turn and leap back again.

Many naturalists who have seen this behavior have concluded that it is a playful response lacking in any practical outcome (Gudger, 1944). Other observers have noted that fishes which persistently leap over floating sticks are often heavily infested with ectoparasites that are easily scraped off. It has been suggested that leap-

ing across solid objects may serve to dislodge the parasites, and thus to free the fish of the infestation (Breder, 1932). The validity of this surmise has yet to be established by additional observation or by experimental approach; but the significant point would seem to be that it is susceptible to objective verification or disproof. In contrast, it is a very difficult if not impossible task to establish beyond reasonable doubt the absence of utilitarian function for any type of animal response.

Adoption of the non-utilitarianism criterion in its pure form reflects a certain degree of naiveté. As has been noted, young animals often perform, incompletely, various actions which will be executed in their totality during adult life. In the mature animal the behavior in question can be shown to serve an obvious and biologically useful end, such as mating and reproducing, securing food, self-defense, etc. In the young animal the behavior pattern does not terminate in the same result. Accordingly it is sometimes concluded that the reactions of the youngster are without any immediate result or purpose.

This is obvious sophistry. There is no reason to assume that a given pattern of behavior must serve one and only one end under all conditions and at all stages of development. The flight of a bird may assist it to elude a predacious foe, to secure necessary food, to charm its mate, to transport it to a different environment or to bring about any one of several other equally "practical" results. Furthermore, the scientific study of animal behavior, if it has taught us nothing else, should have impressed upon us the folly of trying to define *a priori* the motives and ends of animal conduct. It is unadulterated nonsense to assume that, in the absence of intensive and prolonged study, the human observer is capable of discerning the presence or absence of a "useful" result consequent to a complex response. (The eating of bones by pregnant female mammals of non-carnivorous species was thought useless until advanced understanding of the physiology of pregnancy revealed the need for extra supplies of calcium.)

The practicality or usefulness of a course of action is

a function of a multiplicity of variables. A man transported suddenly into a new and strange cultural setting would be at a loss to recognize the motives for certain response patterns, and might be quite incapable of discriminating between utilitarian and non-utilitarian modes of conduct. The building up of a comfortable financial reserve in anticipation of future emergencies is a practical and utilitarian bit of behavior in our culture. The same behavior would be highly impractical not to say socially dangerous among Mexicans of the Sinaloa region; for in their culture a man is responsible for the support of all relatives whose resources are inferior to his own. Therefore the individual with wealth or a new house is perpetually parasitized by less fortunate relatives who continue with him as long as the money lasts or the house stands. Thus the accumulation of "excess" worldly goods is practical in one social setting and quite the opposite in another.

If, without extensive study, man can not differentiate between "useful" and "useless" behavior in fellow members of his own species, how can he expect to make such a discrimination in connection with the reactions of animals of an entirely different genus, and even class?

Results of Play

Although many writers agree that playful acts must be performed because of the pleasure or satisfaction which they engender, and can not have any immediate, utilitarian outcome, it is nevertheless often stated that certain types of play do possess important, long-term effects.

Youthful practise for adult life. It is common knowledge that immature animals frequently perform incompletely or imperfectly, and without apparent useful outcome, certain patterns of behavior which will be exhibited during adulthood in complete and biologically effective form. This observation has so impressed many writers that they interpret one function of the play of young animals as "an irresponsible apprenticeship to the serious business of life" (Pycraft, 1912; Mitchell, 1912).

Adherents of this view usually make several basic as-

sumptions. (1) The type of play to which this theory pertains is held to be determined largely by heredity, since it is believed to appear without opportunity for learning or imitation, and takes approximately the same form in all members of a given species. (2) Although instinct accounts for its broad outlines, the response is regarded as being imperfectly organized upon a purely genetic basis, so that each individual must perfect the inherited reactions by practice and repetition. (3) An intriguing ramification of the theory is stated in the further postulate that the types of behavior under consideration are all of great biological importance, since each is essential to the life of the individual and thus to the perpetuation of the species. It is pointed out that the play period of infancy permits the practice of these vital responses under conditions where error and incompleteness are not fatal. The extension or modification of inherited tendencies is thus possible before the animal is subjected to the exigencies of an independent existence, wherein the forces of natural selection are constantly operating to weed out inefficiency, and the penalty for error may be sudden death (C. L. Morgan, 1900).

It is not impossible that experience gained during the practice of certain activities during youth increases the efficiency with which the same responses will be performed in maturity. However, the observation that the acts are performed incompletely or inexpertly by the young animal, and appear in more complete and biologically-effective form in the behavior repertoire of the adult, does not justify the conclusion that the perfection of the adult's reaction is a result of the practice during immaturity. If we are to prove, rather than assume, that the kitten's repeated chase and capture of the ball of string is later reflected in improved mousing, it must be shown that kittens which have had no opportunity to play at chasing and catching are poorer mouse catchers in adult life than are other cats which have had normal opportunities for such practice during kittenhood. The same comparison holds true for all other types of play which have been assumed to "polish and perfect imperfect instincts."

Unfortunately, objective proof of this nature is almost completely lacking.[1] Perhaps a puppy which is kept in isolation from all other animals, and thus prevented from indulging in sham fights, will, upon the attainment of maturity, be equally as ferocious and successful a fighter as other dogs which participated in countless mock battles during puppyhood. These suggestions run counter to the interpretation of play as a form of essential training and preparation for adult life; but the important point is that we simply do not know which supposition most closely approximates the facts. Only direct test will settle the question.

In a few instances there is good reason to believe that the "playful" execution of a behavior pattern during immaturity is without effect so far as the performance of the same response in adulthood is concerned. For example, during their wrestling, chasing and mock-fighting immature rats often execute large portions of the adult mating pattern (Small, 1899; Beach, 1942a). If, however, rats are raised in individual cages, so that they have no opportunity for any such practice, they mate during adult life in exactly the same fashion and with the same effectiveness as do their brothers which have been raised with females (Stone, 1922; Beach, 1942b).

This is not to say that the infantile practice of various behavioral reactions is always without effect upon the efficiency with which the responses are executed later in life. The conditions under which a kitten is raised have a powerful effect upon its tendency to kill rats (Rogers, 1932; Kuo, 1938). Some kittens fail to develop rat-killing behavior when raised in isolation but display such reactions after they have observed rat-chasing and killing on the part of another cat (Kuo, 1930).

The play period of some primates is prolonged, and involves the execution of many activities later indulged in by the adult (Yerkes and Tomlin, 1935). It is known that sexually inexperienced adult male chimpanzees often

[1] As a matter of fact, young kittens which "play" with rats are less likely to become rat killers when they mature than are kittens that fail to exhibit mock chases or capture responses (Kuo, 1930).

are incapable of mating effectively with the receptive female. Apparently a great deal of experimentation and practice is necessary before this vital part of the animal's behavior repertoire can be carried out efficiently; and Bingham (1928) has found that immature chimpanzees exhibit sex play very frequently during childhood. It is not too much to assume that this practice has its beneficial effects upon adult performance. However, to assume is not to know, and in this case, as in every other, direct test of the hypothesis offers the only means of arriving at a final answer.

A point sometimes overlooked by adherents to the theory that play serves a preparatory function is the occurrence of similar responses in adult animals. Cooper (1942) has described the play of mature African lions as consisting chiefly of hiding behind objects and then creeping forth to stalk and perhaps leap upon another adult. Presumably the grown animal has no need to practice such activities (although it would undoubtedly be suggested by some authors that this behavior is a means of keeping the responses in good working order!); but of course the fact that such playful reactions occur in adult life does not prevent them from serving a preparatory function in the juvenile animal.

Exploration and experimentation. Exploratory play is sometimes held to familiarize the animal with the properties and potentialities of the world about it. An eventually practical outcome of such play has been thought to lie in its tendency to promote the development of new modes of conduct and to inhibit biologically dangerous reactions. From the psychiatric point of view, Masserman (1944) has suggested that exploratory responses represent one expression of an anticipatory need to determine the relative safety and potentialities of the environment. Although these assumed functions of exploratory play are based upon *a priori* reasoning more than controlled observation, there are some instances in which they can be shown to exist.

Kohler (1931) reports that captive chimpanzees given stout sticks or poles soon devised a crude form of vault-

ing or jumping, using the stick as a crutch. Originally this response was indulged in apparently as a form of amusement, and was not used as a means of achieving any secondary objective as far as the observer could determine. Although further test and observation would be necessary to establish the point, it seems probable that the pole-vaulting response was a form of play, and the outgrowth of experimentation with the stick. Later, however, when the apes were confronted with the problem of obtaining a banana which was suspended above their reach they quickly put the vaulting technique to good use, employing it as a means of getting the fruit.

Socialization. Some kinds of play have been assumed to encourage particular types of inter-individual reactions. It will be recalled that chimpanzees engage in various social activities which involve participation by several individuals. Tinklepaugh (1940) has proposed that such behavior early in life enhances the individual's adaptability and cooperativeness, both of which are essential characteristics of the species.

Self-expression or diversion. Yerkes (1943) states that play in chimpanzees is one form of self-expression, self-amusement or diversion. He has observed animals draping themselves and wearing strips of cloth or paper, fruit skins, flowering plants or leafy branches. (Whether or not such reactions can be interpreted as self-adornment is a moot point; but the element of diversion is held to be obvious.) Apes often "paint" or smear objects or flat surfaces with feces, and this too is a form of activity which Yerkes regards as self-expressive, and perhaps playful.

Kohler (1931) describes the manner in which chimpanzees moistened white clay with saliva and then proceeded to daub the resulting mixture on their own bodies and upon all sorts of objects in their environment.

The proposed socialization and diversion functions of certain kinds of play appear reasonable and logical, but must be regarded as speculative until further evidence is forthcoming.

POTENTIAL METHODS OF APPROACH

If it is apparent that current understanding of play in animals is limited, and that presently accepted criteria and explanations are inadequate, it should be equally obvious that there are various steps which could be taken to improve the situation.

Controlled observations. The most pressing need is for controlled observation of those activities which are customarily regarded as play. To replace the anecdotal, impressionistic or romanticized descriptions of animal behavior there must be provided detailed, objective accounts based upon repeated observation. Information is needed, not only concerning the observable reactions of the animal, but also regarding various aspects of the environmental situation. So far we know practically nothing as to the probable stimulus patterns which elicit playful responses.

A beginning in this direction has been made by a few workers. For example, Cooper (1942) reports that the play of lions occurs most commonly following a major change in the environment, such as release of the animals from an inside cage, the introduction of new individuals into the pride or the sudden appearance of the attendant. It is added that play frequently takes place just before feeding time, is more common on cool days, and is shown by females more than males.

Studies of the ontogenetic development and regression of play in a single species would be valuable, and would supplement the vague generalization that play is essentially an infantile activity.

In so far as possible records gathered under field conditions should be checked in a setting permitting systematic variation of the stimulus situation.

Definitions and criteria. In attempting to define or set up criteria for play it should first of all be recognized that no single hypothesis can be formulated to explain all forms of play in every animal species. The types of activity which are commonly termed playful are so vari-

able in form and complexity that a different interpretation is indicated at least for each major category. Secondly, it must be apparent that many playful and non-playful pursuits differ in subtle and elusive fashion. There is no sharp borderline between play and work for animals, any more than for man. The two types of activity are often difficult to distinguish, and some complex responses may be partly play and partly work (Kollarits, 1940).

This means that any serviceable definition of play must be based upon a number of predominating characteristics which combine to set if off from non-playful behavior; and can not be derived from adherence to one or two rigid criteria such as imperfect, juvenile performance or non-utilitarianism. It may eventually prove helpful, if the facts warrant, to state that playful reactions as a class tend to lack the immediate, biologically useful results which normally accompany non-playful responses; but it is definitely inadvisable to set up as an inflexible rule the dictum that no activity is play if it achieves a useful end.

Thirdly, the conclusion is inescapable that play must eventually be defined in objective terms. If no such definition has yet been forthcoming its absence may be traced directly to the lack of essential data. In connection with other, equally complex types of animal behavior, workers are building interpretations founded on recognized, demonstrable physiological and psychological processes and functions. Learning, maternal behavior, courtship and mating, territory defense, social dominance and a host of equally important categories of response have proven susceptible to an objective approach. There is no reason to believe that play is unique in this respect.

Experimental validation of theories. We have previously indicated the necessity of subjecting to direct test certain currently accepted interpretations of the functions of play. There is no need to limit ourselves to speculation in this field. If they actually exist, the "preparatory" function, the "experimental" function and the

"socialization" function which have been assigned to play can be objectively demonstrated, quantitatively measured and operationally defined. Furthermore, as new evidence justifies their formulation, new theories can and should be exposed to the "test-revise-retest" process of critical analysis.

Human applications. In closing it may be worth while to comment on the fact that play in humans, although it has been studied more extensively than play in animals, is only partially understood (Alverdes, 1932; Blumenfeld, 1941; Britt and Janus, 1941; Curti, 1930; Dever, 1917; Watson, 1919). An evolutionary approach has proven fruitful in advancing our knowledge of many phases of human behavior; and it is not too much to hope that the careful study of animal play will offer potentially significant results in the increased understanding of similar behavior in man.

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THE ANGLER-FISHES, *LOPHIUS PISCATORIUS* ET *AMERICANUS*, USE THE LURE IN FISHING

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Lophius is found in the North Atlantic, off the Atlantic (and Mediterranean) shores of Europe and off those of Eastern North America. Linnaeus early gave the European fish the name *L. piscatorius,* and the American form has been thought to be identical and was from the first given the same appellation. However, as early as 1837, Valenciennes found that the American fish differed from the European form in certain external features—in the teeth, lower lip and the presence of small eye-like spots on the back. These unlikenesses led him to propose for the Western Atlantic fish the specific name, *americanus.*

·However, the findings of Valenciennes were considered too insignificant for this species differentiation, and the names *L. piscatorius* was affirmed the correct one until recently. In 1928 and in 1929, irrefutable evidence was produced leading to a return to the name given by Valenciennes to the American fish.

In 1928, Marshall and Grafflin, by microscopical studies of the kidneys of adult specimens from Europe and the United States, found totally unlike structures in certain parts of these organs. And in the following year (1929) Berrill, studying the embryology of the American form, found that the eggs are smaller than those of the European fish. More marked differences were found in the development of certain relatively identical stages of the larvae of the two forms. These clearly demonstrated differences necessitate a return to the name given by Valenciennes, and make it necessary that the feeding habits of the two forms be considered separately.

The European Angler, Lophius piscatorius, Uses its Lure in Fishing

As may be seen from Yarrell's figure (1841), reproduced here as Fig. 1, Lophius is large forward (length

and breadth of the head being about equal), and falls away rapidly behind to a relatively insignificant tail and caudal fin. Because of this tadpole-like make-up, our fish was called *Rana piscatrix* (fishing frog) by the ichthyologists of the 1500's. The head is very depressed and the large staring eyes have been brought close together onto its flat top. The huge mouth (nearly equal in width to the head) is terminal and somewhat uptilted, and both jaws are thickly beset with long, pointed, backwardly-slanting

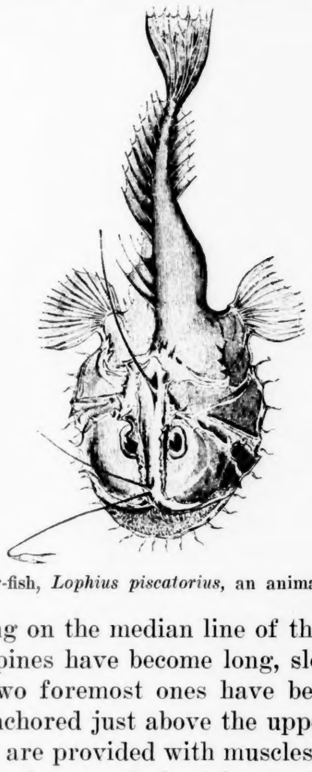

FIG. 1. The Angler-fish, *Lophius piscatorius*, an animate piscine fish-trap.

teeth. Standing on the median line of the head, the anterior dorsal spines have become long, slender and flexible, and the two foremost ones have been transferred forward and anchored just above the upper jaw. These two whiplashes are provided with muscles at their bases, and by these can be moved about in any direction. The anterior one has at the tip a fleshy lappet or "bait"—here shown as forked.

Yarrell's figure is not the best I know, but it shows the flat wide head with the dorsally placed eyes and the tentacles located almost on the upper jaw. And, better than

any other accessible figure, it shows the anterior tentacle with its bifid lure hanging on front but to the right of the center of the mouth with its armament of teeth. From this it will be seen that *a priori* the angler looks to be one of the best animate fish traps in the piscine world.

For our earliest knowledge of the angling habits of this fish, we must go back to the father of natural history, Aristotle (384–322 B.C.). Aristotle must have known the fish at first hand, since he so accurately describes its make-up and its actions. I quote from Sir D'Arcy W. Thompson's translation ("Historia Animalium," Oxford, 1910):

After the general remark that "In marine creatures, also, one may observe many ingenious devices adapted to the circumstances of their lives," then for our fish Aristotle continues thus:

> The accounts commonly given of the so-called fishing frog are quite true. . . . The fishing frog has a set of filaments that project in front of its eyes; they are long and thin like hairs and are round at the tips; they lie on either side, and are used as baits. Accordingly, when the animal stirs up a place full of sand and mud and conceals itself therein, it raises its filaments and, when the little fish strike against these, it draws them underneath into its mouth. . . . Furthermore, the fishing frog is unusually thin when he is caught after losing the tips of his filaments.

The reader will note the significance of Aristotle's final sentence. It shows in what thoroughly scientific fashion he studied this fishing habit. This final statement definitely "clinches" the matter that the lure is of especial use in the catching of food.

From Aristotle's day to the present (a time-span of over 2,000 years), people (scientific and otherwise) have quoted Aristotle only to cast doubts on the accuracy of his observations. From a study of the make-up of Lophius, all are agreed that *a priori* he must catch fishes by the use of the lure. But, since Aristotle, until very recently no man—scientific or lay—could say, "I have seen the angler-fish angle with his lure." And because no one had actually seen it, Aristotle's account was at the best doubtfully accepted. But it seems incredible that in all these long years no one, out in open water or in an aquarium tank, has seen Lophius fishing with the lure.

But at long last *Lophius piscatorius* has been observed while doing this very thing. W. C. Chadwick has seen and briefly described (1929) the feeding "on many occasions" in the tanks of the Marine Biological Station at Port Erin, Isle of Man. Some living young specimens of the coalfish, *Gadus virens,* were introduced on many various days into the tank with the Lophius. Here were its reactions as recorded by Chadwick:

These [fish] would soon be noticed by the angler, which, while remaining stationary with closed mouth, raised the lure from its horizontal position along the back and jerked it to and fro. Suddenly, as the unsuspecting coalfish hovered over the head of the angler and sampled [to sample?] the living and actively moving bait—I cannot say that I ever saw it touch the bait with its snout—the angler's mouth would open and as suddenly close upon its prey; the head of the coalfish always disappeared first, while the tail projected from the tightly closed mouth. A few seconds later the tail would be drawn by a sort of suction into the still closed mouth and the angler would be ready for another meal.

The angler was never observed to pursue its prey, but would lie perfectly still on the bottom of the tank. However, when the coalfish were introduced the lure would be "actively jerked to and fro." But when no prey was in sight, the lure would be laid horizontally back on top of the angler's head.

Here then is the long-wished-for proof that the lure is used in fishing. And at long last Aristotle is corroborated.

In 1937, D. P. Wilson published "The Habits of the Angler-fish, *Lophius piscatorius* L., in the Plymouth Aquarium." This account of the habits of a fish, very difficult to maintain in an aquarium, is so full, so clear, so complete, that it is a joy to the student of fish habits and behavior. Of the particular habit of interest here, Wilson gives individual histories of three small specimens which lived in the tanks for months and were often seen to angle with the lure. Another was seen to hold the rod over the closed mouth in readiness to fish but was not actually seen to catch anything.

The whole paper is very interesting, but here is what Wilson writes of the angling:

An angler when hungry erects the lure immediately any suitable fishes come anywhere near and endeavor to attract one of them close enough to be

caught. The lure is quickly jerked to and fro and, as the rod is almost invisible, the bait (in my specimens always forked and 'fly-like' not vermiform) simulates some tiny creature darting about. An attracted fish rushes up in an endeavor to catch it; the bait is skillfully flicked out of its way just in time and, with a final cast, is dashed down in front of the mouth which may open very slightly. The intended victim, still following the bait, turns slightly head downward; it is now more or less directly head-on to the angler's mouth. The jaws snap faster than the eye can follow and the tail of the prey is next seen disappearing from sight through the firmly closed mouth. As far as I have been able to observe, the bait is not actually touched by the victim before it is caught, as has sometimes been supposed. Touching the bait with forceps does not cause a reflex snapping of the jaws.

The moving lure has a strong attraction for healthy hungry fishes of several kinds. Small pollack, whiting, pout and bass were the species actually observed to be attracted to it, but probably most pelagic fish that capture moving prey by sight would at least swim up to investigate the darting object. Many fish take a ready interest in moving things.

Besides the quick lashing motion of the lure just described, some anglers occasionally combine with it another movement. Every now and then the rod is depressed until the bait hangs just in front of and rather below the level of the lower jaw. It is then for a few minutes given a curious vibratory movement, after which the sharp flicking is again resumed, the bait being jerked over wide arcs in various directions.

The lure, says Wilson, is not always used when prey is to be captured. If a fish happens to swim near the head of the angler it may be engulfed. Anglers vary in the use of the lure—some use it often, some infrequently. When the lure is not in use, it is always laid back between the eyes. "Some individuals were often observed to direct the lure forward horizontally across the mouth, keeping it quite still for hours on end." For this no definite conclusion was arrived at, but hunger was suspected to be the explanation.

The prey, always in front and just above the level of the mouth, is engulfed too rapidly for the human eye to follow. At one moment the prey is trying to seize the bait, the next the angler is sinking down in its sandy bed with the tail of the prey projecting from its mouth, and in the next minute the tail is gone. Thus the fish almost invariably is taken in head first. When the prey is caught broadside on, it has to be worked around until the head goes in first.

These accounts are all very clear and coherent, but some one will make the point that these observations were made of the behavior of small specimens under artificial

conditions in aquariums where the possibly semi-starved fish, restricted in its movements, perhaps behaved abnormally. What is wanted, it will be declared, is an observation of the fish using the lure out in free water under natural conditions—as Aristotle's was.

Such an observation was published in 1925, by Bigelow and Welsh in their "Fishes of the Gulf of Maine" under the name *L. piscatorius*. Parenthetically it may be noted that in 1936 Bigelow and Schroeder changed this name to the present designation. The fishing habits of the American angler-fish in open water will now be described under its new-old and correct name:

The American Angler, Lophius americanus, Uses its Lure in Fishing

Neither Bigelow nor Welsh was so fortunate as to see this fishing, but they quote an eyewitness.

> W. F. Clapp, who has often watched the feeding habits of goosefish [*Lophius americanus*] in Duxbury Bay, Massachusetts, where they are plentiful, describes them to us as lying perfectly motionless among the eelgrass with the tag or "bait" on the tip of the first dorsal ray swaying to and fro over the mouth, either with the current or some voluntary motion so slight as to be invisible. The only fish he has seen them take are tomcod and when one of these chances to approach it usually swims close up to the "bait" but never (in his observation) actually touches it, for, as soon as the victim is within a few inches, the goosefish simply opens its vast mouth and closes it again, engulfing the victim instantaneously.

Then Bigelow and Welsh make the sound remark that "These observations are the more welcome as no other recent student seems to have seen the feeding habits of this species in its natural surroundings." Indeed, they might properly have omitted "recent." As a matter of fact, so far as my search goes, Clapp seems to be the first man known, since Aristotle, to describe the angler's use of its lure in open ocean water. However, his statement is effectually buried in what purports to be purely a systematic work on the "Fishes of the Gulf of Maine." But as a matter of fact this book is for its individual fishes crammed with good natural history notes.

Furthermore, attention is called to the year of publication of Clapp's data—1925. Had his account of the use of the lure by Lophius in natural surroundings been pub-

lished separately under its own proper title, it would by four years have antedated Chadwick's published observation of the angling by a Lophius in an aquarium. However, neither Chadwick's title (1929) nor Wilson's (1937) indicates that the lure was used in fishing. *A priori* one would infer that its use was noted in both sets of observations, but one can not know until the articles have been read. The use should have been stated in each title.

It having been proved by eye witnesses that two species of the genus Lophius use the lure in fishing, it may confidently be expected that other species of this genus, which have a well-formed lure, will have the same feeding habits.

The publication of a historical article like this one has several values. It brings together all the data on the particular subject that can be found by careful search. The distinctive title gets the phenomenon definitely cited in the bibliographies. When read, the article establishes the behavior as a natural phenomenon, and may incite others to publish their like observations—to the enrichment of the literature of the habits and behavior of fishes.

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REVIEWS AND COMMENTS

EDITED BY PROFESSOR CARL L. HUBBS

In these reviews and notices of current biological publications emphasis is given to books and major articles which fall within the special scope of THE AMERICAN NATURALIST, in that they deal with the factors of organic evolution. REVIEWS AND COMMENTS are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as indicated, all items are prepared by Dr. Carl L. Hubbs, Scripps Institution of Oceanography, University of California, La Jolla, California. All opinions are those of the reviewer.

Mainsprings of Civilization. By ELLSWORTH HUNTINGTON. New York: John Wiley and Sons, Inc.; London: Chapman and Hall, Ltd., 1945: i–xii, 1–660, figs. 1–83. $4.75.

ELLSWORTH HUNTINGTON, a leader in the imaginative school of modern geography, has long sought to analyze the interplay of heredity, physical environment and cultural endowment in the determination of human behavior, past and present. In this book he coordinates his previous contributions and adds a wealth of new ideas and facts, in an effort to interpret the fundamental basis of civilization. He draws freely and not inexpertly on the data of evolutionary biology, conventional history, business economics, climatology and other sciences. Although he stretches his vision at times, his views as a rule are judicious and cautious. His more important conclusions are either supported by an extensive mass of critically analyzed data, or are proposed tentatively as working hypotheses. That kind of geography is certainly not to be regarded as unscientific.

The author avoids entanglement in the whirlpool of argument over "races." In the first place he stresses the importance and necessity of environmental and cultural as well as of hereditary factors, without attempting to appraise the relative importance of the three (two?) factors. In the second place he recognizes that racial differences are of much less magnitude than innate individual differences or than differences due to environmental factors, and further emphasizes that each race contains the material out of which progressive advances in

civilization are possible under the stimulus of optimum environment and rigorous selection. In the third place he rightly decries the insane concepts of race that were held by the Nazis (and by members of other arrogant groups), and analyzes the fallacies of the sister concepts of geopolitics. In the fourth place he shies away from discussions of races, by substituting "kith" for race. A kith he describes as a human group held together by intermarriage. But in the broader biological sense, which avoids the conventional and the abused concepts of race as applied to man, a kith is a race, with a degree of integrity commensurate with the degree of interbreeding. The fact that a kith may be of diverse origins does not distinguish it from a race, for the race is the unit of speciation and speciation is often reticulate, probably usually so, to some degree. Even so clear a race as the Tasmanian is termed a kith.

A brief review of the evolution of animal life leads to the conclusion that civilization is characterized by the increasing control of the environment and as such represents the continued operation of a basic evolutionary force. The evolution of man through natural selection is related to the circumstance that man in many ways is a very generalized animal. Cultural as well as organic evolution is attributed to selection. Particular stress is laid not only on the rapid racial improvement of stocks (kiths), through selective processes that are inherent in migrations, but also on the century-long perpetuation of such advances. These conclusions are supported by a extended, data-crammed analysis of the superior qualities of the descendents of early pilgrim families (including the Huntingtons), and by a rather convincing though less thoroughly documented discussion of Icelanders, Jews, Junkers, Indian Parsis, Chinese Hakkas and nomads of various "kiths."

The geographical distribution of civilized qualities in the United States and throughout the world is analyzed and mapped. Consideration is given to the hereditary

bases, particularly those that are attributable to selection during migrations. More emphasis, however, is placed on the rôle of climate as a factor in civilization.

Seasonal variations in human efficiency and culture levels are analyzed at length, as further evidence that the environment controls human behavior. Storms are shown to have major effects on physiological and mental functions. Short-term and global, long-term weather cycles are proved to be real and to have had throughout history great effects on health, business activities and cultural levels. The rise and fall of civilizations, as well as lesser and briefer fluctuations in culture, are interpreted as due at least in part to variations in the environment. Temperature and humidity are indicated as of importance but fail to explain many of the features of cyclic behavior that obviously stem from the milieu. The search for other factors has led to the most pregnant suggestions, proposed guardedly though with obvious favor, that atmospheric electricity and ozone are particularly effective in determining man's level of health, activity, success and progress. In true scientific spirit Huntington grasps for more data to test these revolutionary concepts.

The Life History of an American Naturalist. By FRANCIS B. SUMNER, Lancaster, Pa.: The Jaques Cattell Press, 1945: i–viii, 1–298. $3.00.

THE last of the many cherished conversations I had with FRANCIS BERTODY SUMNER so well exemplified his intellectual honesty—a ruling force in his life—that I risk an overly personal touch by recounting the gist of his remarks. During a visit at the local hospital, where he went for observation on one of the several short illnesses that preceded his death on September 6, we naturally discussed his autobiography, which had just come off the press. As I was leaving he called me back from the door to remind me of the frankness that I at times display in reviews and to insist that I allow no personal feelings to

inhibit me from expressing exactly what I think of the book. He had told the story of his own life as a vehicle for the expression of his long-considered views on the biology and sociology of man. He had reached out for a wider audience and he yearned for a favorable reception of his ideas, yet he called for unhampered criticism.

In compliance with "F.B."'s last request I will say that some readers, including close friends, take exception to certain views that are expressed in this almost wholly uninhibited and searchingly self-critical autobiography. A few are amazed that he should have analyzed so frankly what he regarded as defects of his own parents, in his effort to estimate the interplay of heredity and environment in determining the weak as well as the strong aspects of his own personality. Others are made unhappy by his repudiation of conventional religious beliefs. Some fellow citizens of southern California will probably dislike the violence of his attack on the booster. Other readers will regret the frankness of his views regarding the unlikable traits which he held to characterize Jews to a greater extent than Gentiles. I imagine there may even be lay readers who will decry his attacks on anti-vivisectionists. A considerable proportion of fellow scientists may ridicule his leanings toward "extrasensory perception" as well as the lingering remnant of his former favorable attitude toward Lamarckism. Despite his keenness and success in experimentation some biologists will belittle his sustained interest in observational natural history.

Such feelings of shock or repugnance I do not share, though I do not wholly agree with all of the views expressed in the thought-crammed book. The unquestionable honesty and frankness of the author smooth down the points of disagreement. When, as often, his ideas lean backward away from conventional viewpoints I appreciate the great force of his free thinking, the rigorousness of his objectivism, and the hypertrophy of his critical judgment, particularly toward himself.

It was obviously these qualities of man and scientist, all revolving about an intense motive of intellectual honesty, combined with extreme modesty, that led Dr. Sumner to portray himself in a light that does not shine with the fullness of truth, in that he obscured his many outstanding virtues. He was a bit reticent but certainly not the retiring and timid soul that is pictured, for he had many warm friends and a host of admirers. To a far greater extent than most scientists do, he courageously engaged in the service of society. He actively furthered the interests of political and social liberalism, calendar reform, animal experimentation, freedom of science, the conduct of pure research, population control, eugenics, nature preservation, free thinking and release from narrow dogma. He was rather deliberate in speech, and in his book makes note of his greater proficiency in writing, but his conversation was eagerly sought and richly enjoyed. Much of his scientific work was, as he stated, detailed, technical and specialized, but it was widely known, often quoted, and very highly regarded for originality and significance. This is notably true of his epochal researches on speciation in mice of the genus *Peromyscus* and of his studies on physiological and evolutionary adaptations in fishes. Election to fellowship in various societies and academies, to the Vice-Presidency of the American Association for the Advancement of Science, and to membership in the American Philosophical Society and the National Academy of Sciences gave evidence of the esteem in which he was held by his colleagues.

This autobiography is delightfully written, with vivid narratives and with visualizing descriptions of personalities and institutions. Choice humor is there, though it may often need seeking by those who were not personally acquainted with the author. The life story, however, merely provides an interest-sustaining background for the dissemination of views on the unwisdom of some generally accepted customs and beliefs—views that are well

worth the consideration not only of naturalists, but also of any persons who are intelligently interested in human behavior.

What Is Life? The Physical Aspect of the Living Cell. By Erwin Schrödinger. Cambridge: At the University Press; New York: The Macmillan Co., 1945: i–viii, 1–91, figs. 1–12. $1.75.

Before he ventures into the field of biology, in an effort to answer the prime question of life, statistical physicist Schrödinger offers a defense for this act of seeming trespass. He points out the age-old longing for unified, all-embracing knowledge, still felt despite the fact that "it has become next to impossible for a single mind to command more than a small specialized portion of it." He sees "no other escape from this dilemma . . . than that some of us should venture to embark on a synthesis of facts and theories." The apology should be accepted and the author congratulated on his courage as well as insight. The central question he asks is, "How can the events *in space and time* which take place within . . . a living organism be accounted for by physics and chemistry?" "The arrangement of atoms in the most vital parts of an organism and the interplay of these arrangements," he holds to "differ in a fundamental way from all those arrangements of atoms which physicists and chemists have hitherto made the object of their experimental and theoretical research."

The enormous number of atoms in an organism is regarded as consistent with an explanation of its action in terms of statistical physics, though the supposedly somewhat limited number (one or a few million) in a gene renders it difficult, the author thinks, to explain the regularity and permanence of the genetic mechanism. Mutations are interpreted as quantum changes and the physics of life is thereby related to quantum physics. It is held that the permanence of genes leaves no alternative to the theory that genes are molecules. A well-ordered association of atoms is said to be the only conceivable structure

that offers a variety of possible arrangements, sufficiently large to embody a complicated system of determinants within a small spatial boundary. Mutations are regarded as isomeric changes in the gene molecules.

In discussing genetics the importance of differences within the normal range of variation is by implication denied, the rôle of gross mutations is overemphasized and DeVriesian mutations, contrary to views now generally held, are presented as typical ones. The necessity of mutation being a rare event is wisely stressed and the relative permanence of the genes is interestingly attributed to natural selection.

Despite the explanations of life functions in terms of statistical and quantum physics, living matter is held probably to involve laws of physics hitherto unknown, which, when revealed, will form an integral part of physical science. The seeming defiance of entropy through metabolism appears to set life apart, and "the unfolding of events in the life cycle of an organism exhibits . . . orderliness, unrivalled by anything we meet in inanimate matter."

The most essential part of the living cell is held to be the chromosome fibre, which is termed *an aperiodic crystal* in contrast with the *periodic crystals* which physicists have hitherto studied. Whether the distinction is as trenchant as the new terminology suggests, the reviewer is not competent to say, though he would point out that chromosomes are unknown in some of the most primitive organisms and that the distinction between living and non-living matter, and hence between biological and physical laws, may be bridged over by considering such lowly forms of life and the viruses.

The Mosquitoes of New Jersey and Their Control. By THOMAS J. HEADLEE. New Brunswick, N. J.: Rutgers University Press, 1945: i–x, 1–326, pls. 1–16, figs. 1–87. $4.00.

ALTHOUGH it is primarily a guide to mosquito control in New Jersey, professional in its main approach and

somewhat exuberent in the spirit of a public service well accomplished, this volume will also interest systematic entomologists, students of insect behavior and natural history, ecologists, economic zoologists, wildlife workers and conservation administrators, not to mention thousands of folks whose comfort is shattered and whose health is potentially endangered by the Culicidae.

Correct identification and a knowledge of the life history and flight behavior of each species commonly encountered are stressed as fundamental factors in effective mosquito control. Accordingly, about two hundred pages are devoted to a detailed treatment of the species, under six ecological groups: salt marsh breeding, household, fresh-water swamp, malarial, woodland pool and miscellaneous. The typical treatment gives the scientific and the vernacular name; the range in terms that are too brief and too general; the number collected in New Jersey, from an introductory tabulation of 1,056,628 specimens trapped from 1932 to 1941; hand-lens recognition characters; description of the adult, with a good figure; habits of the adult, with brief accounts of the breeding behavior, biting proclivities, and vagility; description of the larva, particularly detailed and well illustrated; and habits of the early stages, described at length and emphasizing points of concern to ecologists as well as to mosquito control officials. Special emphasis is properly given to the larvae, which are of critical significance in control operations.

This main section is taken bodily from John B. Smith's bulletin of 1904, with slight emendations and small additions. It covers the 37 species of Culicidae other than "*Corethra*" (*Chaoborus*) that were known from New Jersey in 1904, but barely mentions the 4 species that have since been found in the state. It is indeed a tribute to Dr. Smith's energetic and pioneering work that his treatise can be reused, but it would seem that many of the personal observations and reflections could have been abbreviated to make room for further data and conclu-

sions from forty years of mosquito research and control operations.

The first chapter, "Value of Mosquito Control," contains little more than a brief history of the mosquitoes of New Jersey as pests, and leaves to a later chapter the history of control, which is treated from the viewpoint of personalities. Statistical data on the efficacy of mosquito control in New Jersey are so extremely brief as to carry little convincement. Perhaps the results are self-evident to New Jersey residents; but perhaps, as is commonly true in wildlife operations, too small a proportion of the funds and energy expended has gone into a critical evaluation of the results. Almost no consideration is anywhere given to the debit side of the ledger, particularly to the destructive effects that the extensive drainage of marshes may have had on the feeding grounds for waterfowl, on the nursery waters of food and game fishes, or on natural habitats for the pleasurable observation and scientific study of wildlife. In wildlife administration there is obvious need for the joint consideration of all such natural assets.

There can of course be little doubt that the partial elimination of these insect pests has been a great boon in metropolitan and resort areas, but the claims that are made in regard to the financial value of mosquito control in New Jersey appear to credit too much of the rise in property values to such control. It is only natural of course that those who are vigorously and professionally engaged in this socially beneficial activity should see with somewhat biased eyes.

Evidence on the virtual elimination of malaria through mosquito control, in localities where it has reappeared, is presented in the final paragraph of the book, but so briefly as to incite queries in the mind of the critical reader, even though no doubts were left in the author's mind. Otherwise malaria is scarcely mentioned, beyond a five-line passage in the account of the chief vector. Why malaria in New Jersey as in other regions declined

to insignificance following a high incidence in early years is not discussed. Nor is there any mention of the possibility that new and virulent types of malaria may be introduced by soldiers returning from malarial areas.

The standard method of mosquito control in the salt marsh areas of New Jersey, where the problem is most acute, is a very interesting example of applied ecology. Briefly the procedure is to alter the marsh drainage, by ditches and tide gates, so as to give the natural enemies of the mosquito larvae access to the mosquito breeding waters at almost all times (but not necessarily for periods shorter than the larval life of the pests). The main enemies are the native killifishes, chiefly species of *Fundulus*. Some efforts have been made to introduce into New Jersey the mosquitofish *Gambusia* which has proved to be a highly effective control agent in many parts of the world. These trial introductions have mostly failed, probably largely because the fish were introduced from too far south. *Gambusia* has recently been successfully acclimated in northern Illinois and in Michigan by a gradual process of the northward extension of its range. The winter-resisting stock thus produced may prove an aid in the further control of mosquitoes in New Jersey and other northern states.

NOTICES OF NEW BOOKS

They Hop and Crawl. By PERCY A. MORRIS. Lancaster, Pa.: The Jaques Cattell Press, 1945: i–xiv, 1–253, many figs. 2nd ed. $3.50.—This most recent of books in the "Humanizing Science" series concerns the descriptions and habits of some of the reptiles and amphibians of the United States—more properly, the eastern United States for the Connecticut-born author draws scarcely at all upon the wealth of material west of the Rockies. The illustrations are excellent, leaving no doubt as to Mr. Morris' superb abilities as a photographer of difficult subjects, and the pronouncedly informal style is readable and non-technical. The great number of errors which marred the first edition (1944) have been substantially reduced; nevertheless there remain a goodly number of minor ones which will bother schooled sys-

tematists but will remain undetected, happily, by that great majority for whom the book is obviously intended.—NORMAN HARTWEG, *Museum of Zoology, University of Michigan, Ann Arbor, Mich.*

Optical Instruments. By EARLE B. BROWN. Brooklyn: Chemical Publishing Co., 1945: i–xii, 1–567, figs. 1–211, A–S. $10.00.—The basic principles of design, function and adjustment of the various common types of optical instruments are presented in this volume for the benefit of student, operator, teacher, engineer and repairman, rather than for the optical or mechanical engineer. Considerable space is given to the theoretical discussion of optics, written in a moderately technical but understandable style, with the more complex mathematical proofs relegated to an appendix. There follows a main section on the description, operation and theory of optical instruments—telescope, cameras, microscope, field glasses and binoculars, projectors, spectroscope, theodolites and others, with special treatment of military instruments and range finders. The third part deals with the construction and maintenance of the instruments. Supplementary topics are the design of optical systems, the manufacture of optical glass, of general interest, notes on physical optics. The useful volume ends with a glossary of optical instrument terms and a comprehensive index.

Principles of Modern Biology. By DOUGLAS MARSLAND. A Complete Reconstruction and Modernization of CHARLES R. PLUNKETT's Elements of Modern Biology. New York: Henry Holt and Co., 1945: i–ix, 1–774, figs. 1–350. $3.75.—College teachers who wish to or are willing to displace the natural history or the morphological approach will find in this "reconstructed and modernized" text an excellent aid in elementary instruction in biology. The opening section exposes the student to the principles of nutrition, responsiveness and reproduction and these basic concepts are returned to in subsequent sections. Consistently the emphasis is physicochemical and experimental. Anatomy, to a large extent human, is presented only as scattered adjuncts to the physiological discussions. There is little basis for an appreciation of structural organization, either individual or comparative. Observation is defined as merely the first of four steps in "the scientific method," without any suggestion that

some branches of the life sciences—paleontology and human genetics for example—have made great progress in themselves and substantial contributions to general biology, almost entirely without the advantages of controlled experiments.

There is a rather extensive and adequate treatment of heredity, leading to a short consideration of embryonic organizers and the nature of the gene. Speciation is held to be a very gradual process. Natural selection is presented favorably in very general terms, whereas Lamarckism is briefly treated as a disproved theory of evolution. Although labelled "The Consequences of Evolution" the final chapter deals with taxonomy, comparative anatomy, embryology, biochemical relationships and the fossil record as evidences of evolution—all within 27 pages. The classification of plants and animals is relegated to an appendix of 6 pages, followed by a glossary and an index.

A rather high standard of accuracy has been maintained, but a few misleading statements were noted. For example the number of species of chordates is given as 30,000, whereas there are about that many species in the Pisces alone. The increased brain size in vertebrates is illustrated by a figure, to one scale, of the brains of frog, cat and man, without qualification as to size of animal. "Varieties" is used where "subspecies" would be preferable. The electric ray and the "stinging ray" are confused.

As a rule the presentation is superior. The diction is clear and decisive. Choice of subject material has obviously been carefully considered. The explanatory comparisons will catch the interest of modern youth. The text is well illustrated by zinc figures, but the half-tones are dull and lifeless, due perhaps to the war-quality paper. May it soon improve!

SHORTER ARTICLES AND DISCUSSION

SURFACE-MASS RATIO, PALEOCLIMATE AND HEAT STERILITY

For the past few years I have been much interested in temperature trends with respect to the phenomenon of archosaurian extinction, and originally I attributed their disappearance to the possible occurrence of excessively high environmental temperatures acting on the somatic tissue (Cowles, 1939, 1940). In supporting this thesis it was suggested that, because of the climatic conditions presumed to exist as their thermal environment, it was as reasonable to ascribe to fur and feathers the original role of heat exclusion as to insist on their exclusive function as heat-retaining mechanisms. Similarly, the trend in the archosaurian size and changing surface-mass ratio was described as a device to escape deleterious heat effects through the acquisition of progressively smaller surface areas through which to absorb heat and thereby warm the proportionately larger mass of the organisms.

Following the appearance of these articles, objections to the theory were made on the ground that there was no tangible evidence for the existence of either rising or high temperatures and that in fact the consensus of thought agreed on a slowly descending temperature, although the ground for such a supposition seemed open to question.

In spite of the objections based on the absence of tangible evidence for the past existence of high temperatures, the problem continued to receive attention and study, with ultimate result that evidence for thermally induced sterility (Cowles, 1945a, 1945b) accumulated to the point where its apparently universal occurrence could no longer be ignored and this phenomenon of a very heat-sensitive male germ plasm and a more heat-resistant body was substituted for the original concept of heat damage to the body, that is, to the somatic tissues.

Up to the present I have neither received nor seen any objections to this modified viewpoint, but there still remains the question as to whether temperatures had actually risen or fallen during the Cretaceous and immediate post-Cretaceous time.

From the subtle nature of the evidence for this possible cli-

matic trend, it is probable that we must look to biological sources for evidence concerning types of climatic changes that in the nature of things could neither produce nor leave any gross mechanical evidence of their occurrence, such as those left by glaciation.

Up to recently I have been forced to rely in part on the presence in the Cretaceous of corals and tropical vegetation, palm and figs, as far north as Alaska and as far south as Tierra del Fuego to support this theory. Certainly this invasion of areas now characterized by frigid conditions would lead one to suppose that the absence of the tempering effect of a heat-reflecting ice cap, which permitted this invasion, would allow considerably higher temperatures to prevail in what is now called the temperate zone. However, it is commonly contended that the character of plant and animal distribution is merely indicative of the absence of the highly zonal climates of to-day and that the absence of a snow and ice cap with its almost total reflection of heat would not have permitted or resulted in the occurrence of higher temperatures to the south, *i.e.*, would merely have made the climate less zonal.

Even though the distribution of organisms may indicate less zonality than exists at present, there is a reason to suggest that, as would be expected without a frigid polar region, temperatures might also have been high. I refer to the Bergmann principle of size trends in the warm-blooded animals. Of great importance is the complementary but reversed condition that is so apparent in the cold-blooded organism, both vertebrate and invertebrates alike.

Bergmann's principle states in effect that warm-blooded organisms of closely related species increase their size with progressive decreases in the environmental temperatures. This trend is a result of a favorable change in the surface-mass ratio, accompanied by great reduction of the bodies' heat-radiating surface while the heat-producing mass becomes proportionately larger. The saving in energy requirements, *i.e.*, in heat or temperature maintenance, thus tends to foster larger size in colder climates. This effect may be readily envisaged by comparing the rate at which a teaspoonful of hot water will cool to the temperature of the environment, with the rate for a pint, quart or gallon. The underlying principle is the same in both the example and in animals. Therefore, according to the Bergmann

principle, because of this differential heat loss, closely related species are larger as they advance into arctic or alpine conditions.

Similarly, while it has been recognized that reptiles decrease in size with progress to colder areas, and that only the smallest lizards or the young of larger but not largest species remain active throughout even southern California's bland desert winters (Cowles and Bogert, 1944; Cowles, 1941), the importance of this trend appears to have been overlooked.

At first glance the logical basis for this trend and the desirability of its incorporation with the Bergmann principle is not apparent, but if one considers the source of heat in the endotherms —the warm-bloods—where excessive heat loss is equivalent to energy loss and exhaustion, with the condition in the ectotherms where heat loss does not represent energy loss, and in which heat is absorbed freely *through the surface*, then in cold climates the favoring effect of small volume and large heat-absorbing surface at once becomes apparent, and one principle complements the other.

Thus it is logical that whenever heat must be absorbed dermally, that is, as in the ectotherms, then the smallest forms of closely related species as in reptilian families, will be found extending their range northward and southward from the equator and its consistently warm climate. That this is the result of favorable changes in the surface-mass ratio can scarcely be doubted.

As has been pointed out in an earlier paper (*supra cit.*) the advantages of small size are numerous and include, amongst other things, a very rapid warming of the body through favorable relationship of large surface in proportion to a relatively small mass and also the ability to use very much smaller food particles which, because of a favorable surface-mass ratio, will digest more rapidly than will the bulkier amounts and sizes of food required for maintenance of larger organisms.

With progression toward the tropics, more abundant and more constant supplies of heat permit an ever-increasing body size in the ectotherms because rapid warming becomes a less important factor owing to the favorable surrounding climate. For these reasons it is only in the tropics, where temperatures are equable and heat-absorption equals heat-loss (because days and nights are equal) that we find our largest reptiles. Almost any family

of the Reptilia will suffice for examples, but a few may be mentioned, such as the Iguanidae, Boidae and the Varanidae. These few families are selected because they will probably be familiar to most biologists as well as to workers in other fields.

In the light of facts concerning body size and its relation to the thermal environment, we see that Bergmann's principle with respect to the warm-bloods and also the condition in the reptiles, are both based on the factor of heat economy and heat regulation in terms of favorable changes in the surface-mass ratio.

It is essential to recognize the fact that the trend in the two groups, while apparently opposite in character, is essentially identical because it is based solely on the nature of the heat source, that is, as to whether heat is derived from within through the efforts of the organisms, and must be conserved, or whether the heat is received from without, entailing no energy expenditure. In either case body temperature is obtained or sustained to an effective degree by adjustment through favorable surface-mass ratios.

At this point one may logically ask as to just how these factors fit into an interpretation of paleo-climates. If we apply Bergmann's principle to the warm-bloods in a chronological pattern—linear in time rather than latitudinal in arrangement, we find a steady increase in size in the evolution of such well-known genera as the horses, elephants and other mammals, apparently accompanying falling temperatures that were climaxed by Pleistocene glaciation. Will Bergmann's principle be admitted as pertinent evidence of climatic trends in this case, or will it be rejected? Can one reject the nature of the evidence in the chronological-Paleontological distribution of body size, yet accept it in the case of latitudinal distribution when the parallel is so similar? Then if Bergmann's principle is acceptable with respect to the mammals as applied both to latitudinal and chronological series, what inference can be drawn from the fact of size increase other than that it describes climatic changes? If it is assumed that the similarity is merely accidental and has no bearing on paleo-climatic trends, we must also reject the evidence supporting the Bergmann principle, as well as other no less well-supported ecological principles.

In discussing the Reptilia, the general pattern of a reversed size trend seems to be as reliable, and the principles the same

as where the Bergmann principle is applied to the warm-blooded animals. Thus the same surface-mass factor is in operation, and, as we have seen by the trend with respect to falling temperatures, is merely the complementary reverse of that in the warm-bloods, and the explanation is obvious and logical. If then we apply the principle as found in the Reptilia, and use this in attempting to determine temperature trends through the evolutionary development of reptiles, what inferences can be drawn? Can we reject the implication seemingly involved in the size trends in the Reptilia, and consider them inapplicable, while we accept the same factor in the warm-bloods?

It seems reasonable to interpret the enormous size reached by some of the archosaurs as evidence that high temperature must have prevailed in their day just as to-day in living reptiles size increase accompanies temperature increase. Our only other assumption would be that the archosaurs could have conserved even the relatively little internally generated heat and through the exaggerated surface-mass ratios have become essentially "homoiothermous" but not endothermic or warm-blooded. However, it is obvious that this condition could not have eventuated without high environmental temperatures existing while the organisms were en route to this denouement.

The enormous size of a few species must be assumed to have been favored by climatic changes, while other factors such as genetic composition, behavior and change in habits or habitat, that is adjustments as we see them in the living ectotherms to-day, permitted the survival of the smaller species along with the larger forms.

Although the trend towards large size may have reflected climatic conditions, this may not mean that environmental temperatures were exactly proportional to the increase in size, although this may be possible. That is, body temperatures may not have been so extremely high except in the summer when the long days, exceeding by many hours the cooling nights, may have resulted in a daily incremental accession of heat, with a tendency towards ever higher body temperatures. This result might be attained through failure to radiate the daily gain during the short nights.

An important factor that may not be at once apparent is that a size increase of the extent seen in many of the archosaurs may

actually represent not a heat-conserving development but a heat-protective device, and that the huge bulk, with resulting small surface area, limited the temperature which they could achieve.

In view of the dependence of the cold-blooded, that is the ectothermic organisms on their environment for a supply of necessary heat and lack of effective protection except through behavior or mass, we can only conclude that environmental temperatures must have been above those of to-day and in summer probably well above the temperature of the tropics. Such conditions must have been necessary in order to permit the development of the massive bodies and relatively small radiation-absorbing areas of archaic reptiles whose size was greater than that of our present-day tropical species. How these animals would have fared in the ancient temperate zone summers is an interesting question.

Whether or not maximum temperatures reached a level at which they would produce deleterious effects in the somatic cells of the reptiles appears to be of relatively little importance because, as noted earlier in this account and as stated more fully elsewhere (*supra cit.*), the notable heat sensitivity of male germ plasm might have been transgressed, and led to sterility or at least to a greatly reduced fertility.

Although we can probably never know whether these ancient forms, like those of to-day, were also characterized by a heat-sensitive germ plasm, its very universality inevitably raises the question as to whether we may have seen in the demise of the archosaurs a possible failure to maintain fertility resulting from either too high an environmental temperature or an incremental temperature rise and prolonged high temperatures in the bodies of these massive ectotherms.

Although many of the conditions needed for final determination of the role of thermal sterility in extinction may never be revealed, no other explanations for size trends and extinction of many forms of life appear to be more clearly in accord with the implications of the few known facts.

In conclusion, I wish to give credit to those colleagues in the Zoology Department who have so considerately discussed the many problems associated with the new views expressed both in this and earlier papers on thermal effects, and who have so generously contributed supporting suggestions and criticism from

their special fields. In particular I wish to thank those on whom the heaviest burden of the discussions have fallen, namely, Drs. L. H. Miller, A. W. Bellamy and B. Krichesky.

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THE FORCES INFLUENCING CHROMOSOME PAIRING IN *DROSOPHILA MELANOGASTER*

THE nature of the forces responsible for either the somatic pairing or meiotic synapsis of chromosomes is relatively unknown; no hypothesis accounts adequately for the specificity of the pairing of the homologues. Some investigators assume that a specific attraction exists between all homologous loci which results in the point-to-point pairing. This long-range force is usually thought of as chemical in nature. Fabergé (1942), however, has advanced a hypothesis in which a hydrodynamic phenomenon, the Guyot-Bjerknes effect, is utilized. It is supposed that genes are excited into a state of vibration at the beginning of prophase and have then properties of pulsating spheres; *i.e.*, genes vibrating with the same frequency attract one another. Each gene has its own characteristic frequency so that only its own homologue (or homologues) is attracted. Others think that during random movements of the chromosomes there occur chance meetings of some homologous loci. The synapsis of these loci is then followed by a zipper-like closing up of the rest of the chromosome. Lindegren and Bridges (1938) compare the synapsis of chromomeres to the agglutination of bacteria after the addition of antibodies; when molecules of the specific antibody are absorbed by the corresponding chromomeric surface, such chromomeres become capable of adhering to their homologue or homologues. Loci next to agglutinated chromomeres are then likely to touch, and synapsis of the entire chromosome follows.

Evidence concerning the forces involved in synapsis may be obtained by studies on the pairing of larval salivary gland chromosomes of *Drosophila melanogaster* heterozygous for translocations of different lengths. If synapsis is due to specific attraction between homologous loci, one would not expect translocations of different lengths to affect the normal pairing of the chromosomes, provided the homologous segments of the chromosomes were not too far removed in the nucleus to have an effect on each other; the specific attraction between two chromomeres would be expected to exist regardless of the position of the chromomeres in the chromosome complement. Translocations of different length, then, would be expected to show equal frequency of pairing. If the fusion of chromomeres is the result of chance meetings through random movements, however, one would expect a short translocation to be less frequently synapsed than a longer one, for the larger the piece, the greater the chance of at least one pair of chromomeres coming into contact.

Pairing was observed in two stocks heterozygous for a short translocation and in one stock heterozygous for a long translocation in the X-chromosome. In all three cases, the translocation was between the tip of the X and one arm of the second chromosome, the break in the latter being in or next to the chromocenter so that a very short chromosome, the tip of the X, and a very long chromosome, the rest of the X plus the one arm of the second chromosome, were formed.

In both stocks with the short translocation the break in the X-chromosome is at the white locus. In stock white$^{258-34}$ the translocation is between the tip of the X and 2R. The salivary gland chromosomes show the break in the X between 3C3 and 3C5, and in 2R in the chromocenter at 41A. In the second stock, w$^{258-39}$, the tip of the X is translocated to 2L, the break in the X being between 3C3 and 3C5 as in w$^{258-34}$, while the break in 2L is in the chromocenter at 40E and F.

A stock with the break in the X at the cut locus between 7B2 and 7B5 was used as material for the long translocation. The break in the reciprocal chromosome, 2R, is next to the chromocenter between 41E2 and 41E4–5. This stock is designated as ct$^{268-17}$. All three stocks were obtained by Demerec from x-rayed males (Bridges and Brehme, 1944).

To minimize variable factors, larvae of these three stocks were

used which had the normal homologues of the translocated chromosomes from the wild-type Swedish b–6 stock which had been used as the control for the counts. Preparations were stained with aceto-orcein. Determinations of unsynapsed regions were made according to Bridges' 1935 map.

Since 100 nuclei were observed for each stock, figures in the summarized table represent percentages of synapsed and unsynapsed chromosomes as well as actual numbers. For the X tip, translocations w^{258-34} and w^{258-39} gave approximately the same results, each stock showing only 4 per cent. complete synapsis.

TABLE OF ASYNAPSIS

Chromosome	Wild-type			w^{258-34}			w^{258-39}			ct^{268-17}		
X Tip	Complete Synapsis	Partial Synapsis	Complete Asynapsis	Complete Synapsis	Partial Synapsis	Complete Asynapsis	Complete Synapsis	Partial Synapsis	Complete Asynapsis	Complete Synapsis	Partial Synapsis	Complete Asynapsis
Sect. 1—3C3–5	99	1	0	4	4	92	4	0	96	..	..	..
Sect. 1—7B2–5	97	3	0	..	..	..	..	..	..	14	28	58

X Body	Wild-type Asynapsis	Wild-type Synapsis	w^{258-34} Asynapsis	w^{258-34} Synapsis	w^{258-39} Asynapsis	w^{258-39} Synapsis	ct^{268-17} Asynapsis	ct^{268-17} Synapsis
Sect. 3C3–5—20	91	9	94	6	91	9	..	..
Sect. 7B2–5—20	91	9	..	..	..	..	87	13
2L	97	3	88	12	15	85	83	7
2R	89	11	20	80	89	11	17	83
3L	87	13	87	13	88	12	85	15
3R	89	11	92	8	91	9	88	12

In ct^{268-17}, there was 14 per cent. complete synapsis. To test the significance of this difference the formula $t = \frac{p_1 - p_2}{\sqrt{\varepsilon_1^2 + \varepsilon_2^2}}$ (Yule and Kendall, 1937, p. 360) was applied.

The difference was found to be probably not significant. When the data are broken down into cases of partially unsynapsed and completely unsynapsed tips, however, the difference is obviously significant, there being 28 cases of partial synapsis in the ct stock and only 4 in w^{258-34} and 0 in w^{258-39}, and only 56 cases of completely unsynapsed tips in ct^{268-17} as compared with 92 and 96, respectively, in w^{258-34} and w^{258-39}. The pairing of the reciprocal chromosomes of the translocation was equally affected in each stock, 2R giving only 20 per cent. synapsis in w^{258-34}, 17 per cent. in ct^{268-17} and 2L giving 15 per cent. in w^{258-39}. Pairing in the X body and in the chromosomes not involved in the translocation was not affected in any of the translocated stocks.

Though the increase in the occurrence of complete synapsis in the X tip of the long translocation as compared with that in the short translocation was not found to be significant, the much greater frequency of partial synapsis found in the X tip of the long translocation is definitely significant. The results are an indication that the pairing of chromosomes is the result of the chance meetings of some homologous loci during random movement of the chromosomes, rather than the result of a long-range attraction between chromomeres.

The writer is indebted to Dr. K. S. Brehme for her suggestion of the problem and her guidance throughout the course of its study.

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SEASONAL CYCLES AND THE CONCENTRATION OF INVERSIONS IN POPULATIONS OF *DROSOPHILA FUNEBRIS*

The question whether the living conditions to which a species is subject may determine the degree of saturation of a population by chromosomal variants was first raised by Dubinin, Socolov and Tiniakov (1937). Dobzhansky (1943) first showed the direct influence of selection upon inversions in natural populations of *Drosophila pseudoobscura* and demonstrated the dependence of varying concentrations on seasonal cycles.

From the material of our work of 1937, it follows that in the winter (December) population of *Drosophila funebris* in 1936 the concentration of inversion heterozygotes was 75.66 per cent.,

while in August, the period when the same populations had reached its maximum, the concentration was 107.98 per cent.

In 1944 and 1945 three populations within the city of Moscow were examined monthly for the proportions of the inversion II–1. The results appear in Table 1.

These data demonstrate clearly that changes occur in the concentration of inversions in accord with the seasonal cycle. As the populations increased from small densities of spring to enormous sizes at the end of the summer and the beginning of autumn, there occurred a perceptible increase of inversion concentrations. For the Hippodrome population the increase from May to August was 15 times, for the population of the Botanical Garden from

TABLE 1

PERCENTAGE OF INVERSIONS FOUND

Month	Localities* A	B	C	D
March	5.05	....	13.48	...
April	2.72	....	27.73	...
May	0.98	33.72	....	3.44 (n = 29)
June	6.25	44.00	....	0.42 (n = 234)
July	9.42	52.00	43.11	
August	14.75	57.58	41.86	1.70 (n = 530)
September	....	53.19	50.84	0.76 (n = 255)
October	....	....	....	1.68 (n = 238)
November	8.53	....	....	...
Individuals	1,045	501	869	1,286

* A—Hippodrome; B—Botanical Garden of the Moscow State University; C—Obukh Street (Voronzovo Polye); D—the village of Kropotovo.

May to August 1.8 times, for the Voronzovo Polye from March to September 3.7 times.

We have also shown that sharp differences exist in the degree of saturation by inversions of urban and rural populations of *Drosophila funebris* (Dubinin and Tiniakov, 1946). It is of interest that we have not observed seasonal changes of inversion concentrations in the rural populations. At Kropotovo (115 km southeast of Moscow) we have the following proportions of heterozygotes for three inversions (II–1, II–2, IV–1) in different months of the population cycle (see locality D in Table 1). A total of 1,286 individuals was studied; the average proportion of heterozygotes was 1.26 per cent. The different genotypical reactions which urban and rural populations of *D. funebris* exhibit during the progress of the seasonal cycle is of interest, since they indicate hereditary divergence in the process of evolution of urban and rural races of this species.

The facts set forth above give evidence of an energetic selection which has changed the genetic structure of populations in response to changes in habitats. Contrary to the prevailing view that evolution proceeds very slowly, we have observed rapid changes.

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